A study of some of the factors which determine the density and survival of natural populations of the intertidal barnacle, *Balanus balanoides* (L.).

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I INTRODUCTION

A study of the population dynamics of a natural population is usually hampered by the difficulty of measuring the changes in its size and age structure. The usual procedure in measuring mortality is to take a representative sample and calculate the mortality rate from the numerical differences between successive age classes. As Deevey (1947) has pointed out, however, the assumption is made in using this method that the initial numbers and later survival are, for practical purposes, the same from one age class to the next. For many populations this is known to be wrong. The same assumption is necessary for calculating the mortality rate of a population where only the age at death is known. No such assumption is necessary when the survival of a particular group of animals, identifiable in some way, is followed by counts at appropriate intervals.

The possibility of employing this last method governed, in part at least, the choice of Balanus balanoides for this study. It is a sessile intertidal animal and hence, the positions of individuals can be plotted, or counts can be made of marked areas. Successive counts at frequent intervals will then yield an

accurate survival curve for the particular group of individuals. Being intertidal, they are one of the most accessible of marine species so that experiments may be performed in natural surroundings with little disturbance.

This study owes much to the work of Hatton (1938), who made a most comprehensive study of the survival of Balanus balanoides and other intertidal organisms. The present study was undertaken to further analyze the effects of animal interrelations on the survival of barnacles.

A location was chosen at some distance from the motor road in an area little frequented by holiday fishermen. It was located on the extreme tip of Farland Point, Isle of Cumbrae (Full National Grid Reference 26/174541). This proved to be a satisfactory choice, since very few people approached the area even during the height of the holiday season and only two cases of disturbance occured in the two and one-half years of study. Most of the censused squares were located on vertical faces so that they would not be accidently trod upon although some of the lowermost areas were on sloping rocks.

The whole study was carried out on an area of shore about fifty yards long, with an intertidal width

of about fifteen yards. Flat reefs exposed at the lowest tides extended another twenty yards out. The rock, almost entirely composed of Old Red Sandstone, was in the form of N-S ridges about 4-6 feet high, formed by the tilted rock layers. The east side of these ridges was usually vertical, the west sloping, and large boulders were scattered in the ravines between them. Nearby dykes of a dark red basaltic rock, Bostonite, contributed some of the boulders and small chips of flat rock in the ravines.

Except for the reefs just offshore there was no protection from wave action, and the occurrence of Alaria esculenta among the low level algae only at this point on the island indicates that it was exposed at times to moderately heavy surf. Ascophyllum nodosum, a good indicator of low wave exposures, occurred only at the heads of the ravines or on the shoreward sides of the boulders above M.T.L.

Since it was the intention to analyse the effects of predation and space competition on the changes in the barnacle population, the study area was purposely kept small. In this way, it was hoped that such variables as wave action, currents, salinity, sand scouring and other unknown physical factors would be kept somewhat

the same for the various census areas at the same intertidal level. Replicate census squares were established when possible to indicate variability.

All the areas given in this study are projections of irregular rock surfaces on to plane surfaces; if the amount of irregularity is constant, the relative values of density should be comparable. The census squares were chosen on flat surfaces to make them as comparable as possible. All the counts made *in situ* on the shore were done on the same type of rock, Old Red Sandstone. Since this rock is fairly brittle, the removable stones, to be described later, were composed of the Bostonite, which has a finer texture than the sandstone and is much tougher. These had many minor undulations and are probably of the same order of roughness as the sandstone, at least in relation to the size of a newly metamorphosed barnacle.

Assuming the degree of unevenness of the rock to be constant in all the counted areas, the density of a group of barnacles of the same age and size is a simple matter to calculate. Where more than one age group is present, as for example, high in the barnacle zone, the calculation of density is more difficult. Since the only reason for computing density in this study was to indicate

the degrees of crowding in growing barnacles, the area available for growth of a particular age group was the essential measure.

As will be shown later, crowding occurs almost entirely during the first two years when most of the growth takes place. After this time most of the older barnacles simply act as limits to the growth of the younger members. It was decided therefore to calculate the area available to these younger groups by subtracting the area covered by the older individuals from the total mapped area. It must be realized that not all this "available" area is used by the young growing barnacles, but it was felt that it provided a valid estimate for comparison with other areas at similar shore levels where the growth rate is presumably similar.

All the expressions of density refer only to individuals attached to the rock surface; those attached to older barnacles were not used since it is almost impossible to calculate their area of attachment.

To compare the various areas, the census counts have been expressed as numbers per unit of available area. This has been done for the area available for each year group at the initial count for each square.

Then all subsequent counts of this square have been divided by this same area, so that the survival curve is the same as if the original data were used. Each curve represents a particular group of animals.

These survival curves are plotted with the density on a logarithmic scale, the time on a linear scale. In this way, the slope of the curve indicates the relative mortality rate, irrespective of the numbers of individuals involved. This is quite important, since the curves rarely begin at the same density.

Throughout this account, the mean tide levels are indicated by the following abbreviations:

HWS: High water of spring tides.

HWN: High water of neap tides.

MTL: Mid tide level

LWN: Low water of neap tides.

LWS: Low water of spring tides.

II SETTLEMENT

1. Methods.

In studying the settlement of barnacles, previous workers have counted the numbers at intervals during the settlement season. In antifouling work it was usual to expose new surfaces at regular intervals. In some cases the same surface was allowed to accumulate barnacles, counts being made at intervals during the settlement. In this study counts were also made, but it was felt that more information would be secured if individual cyprids could be identified as they attached. When settlement and mortality occur together, a count registers only the algebraic sum of these opposing processes; individual records are needed to separate them. In addition, individual records allow further study of any differences in mortality between early and late settlers or between those settling simultaneously on different types of surface.

Since attached cyprids are small and difficult to see on rocks wet with rain it was decided to attach small flat stones in the intertidal rock which could be brought into the laboratory for examination. These small chips from the dykes were picked up in the intertidal zone and a $\frac{1}{4}$" hole was drilled through each. The method of

attachment of the stone was the same as that used to fasten the wire cages to the intertidal rock to exclude predators. A hole was drilled in the rock $\frac{1}{4}$" in diameter x 1" deep. Then a plastic tube (commercially known as a "Maso-plug") was inserted and a stainless steel screw driven in. One such screw with spacers of stainless steel and plastic "Tufnol" washers was enough to hold each stone in place. The stones and cages remained in place for over two years without losses. The plastic plug allowed quick removal and replacement of the screw. It was found that plugs one size larger than the drill were better. Also, if holes were left empty at high tide animals often crawled in and blocked them up; therefore the screws were always left behind in the holes.

The identification of individual cyprids for future reference was carried out as follows. The stones were brought to the laboratory at low tide and placed outside on the window ledge. They remained there, except for the short examination period, until they were replaced on the shore. The time that they were away from the shore was almost always less than two hours and it was felt that these conditions were very little different from those of normal low tide exposure.

In the laboratory a 2" x 1" glass slide marked in one-half centimetre squares was placed in a position

previously marked on the stone. The examination area was then scanned with a dissecting microscope and all new arrivals, metamorphoses and deaths or losses were plotted on a ruled sheet to a scale about five times natural size. The enlarged scale of the plotting sheet allowed notes to be made. For each stone the same sheet was used throughout each season. The stone was then replaced outside and the next one examined. Without exception during the settlement season the stones were replaced on the shore before that tide rose; in later examinations, after the settlement had finished, the stones were sometimes kept in the laboratory overnight in running sea water.

Between examinations the plotting maps were examined and each new individual was given a grid number which established its identity. The record sheets contained for each cyprid its date of attachment, metamorphosis (or death before metamorphosis) and ultimate date of death. These occurrences were recorded each time the maps were examined.

This method is open to two principal criticisms. Some of the cyprids may have clung to the surface, been recorded and then have swum away at the next high tide. The"clinging reaction" of the cyprids of Balanus balanoides has often been described (Pyefinch 1948) and its

possible role in intertidal settlement has been postulated by Barnes and Powell (1953). However, as Knight-Jones (1953a) has pointed out, the appearance of a permanently attached cyprid is different from one which is clinging by its antennae. The attached one, having poured out its cement, is pulled down and is rounded anteriorly, not pointed as is an unattached cyprid. As a further check, note was made of the cyprids as they were removed from small areas adjacent to the plotted areas on each stone at each examination in the 1954 and 1955 settlement seasons. With a few exceptions all were cemented down; the cement often came away from the stone with the cyprid. When the settlement was dense a few cyprids were noted lodged, often lying on one side, among the other new barnacles. These never metamorphosed and are not included in the analysis of the records.

This system would not record any cyprids which attached and were killed and washed away all in the two high tides between examinations. These omissions are more serious when there are longer intervals between examinations but the error is partly compensated for by the fact that many attached cyprids remain cemented in position for days after death. These would be recorded as having attached but never metamorphosed.

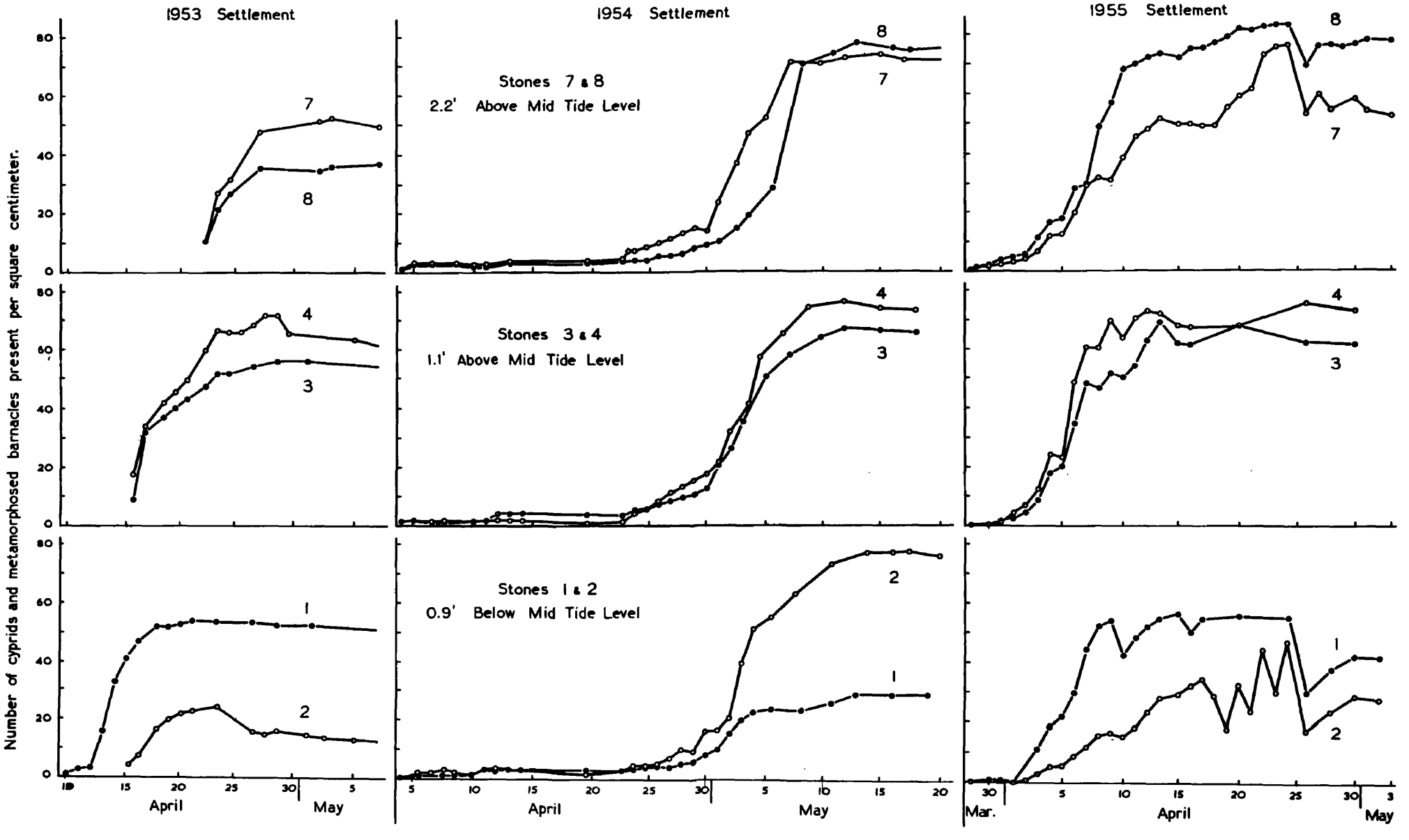
Four pairs of stones were used, one pair at each of four levels from HWN to below MTL. One pair, stones 7 and 8, were adjacent on a vertical face. The other three pairs were placed with the intention of showing the effects of sun and rain; one of each pair was fastened under an overhang of rock, facing down, while the other was placed facing up on a gently sloping ridge at the same level.

The stones were placed out at intervals during the 1953 settlement season, so that the later ones sampled only the last part of the settlement. The stones remained in place for the next two years, thus allowing valid comparisons to be made between the three settlement seasons. Since the 1954 and 1955 seasons were more completely measured, these data were used most in the analysis of the settlement pattern. The data from the highest stones, 5 and 6, ~~is~~ are discussed in section V.

2. Description and analysis of the settlement pattern.

In Figure 1, the gradual accumulation of barnacles during the settlement season is illustrated for the three seasons studied. The settlement begins slowly (except on some of the stones in 1953 when no early records were kept), increases to a maximum and then decreases.

Figure 1. The settlement of Balanus balanoides, shown as the number of living barnacles and cyprids accumulating over the settlement season.


1953 Settlement
1954 Settlement
1955 Settlement
Stones 7 & 8
2.2' Above Mid Tide Level
Stones 3 & 4
1.1' Above Mid Tide Level
Stones 1 & 2
0.9' Below Mid Tide Level
Number of cyprids and metamorphosed barnacles present per square centimeter.
April
May
Mar.

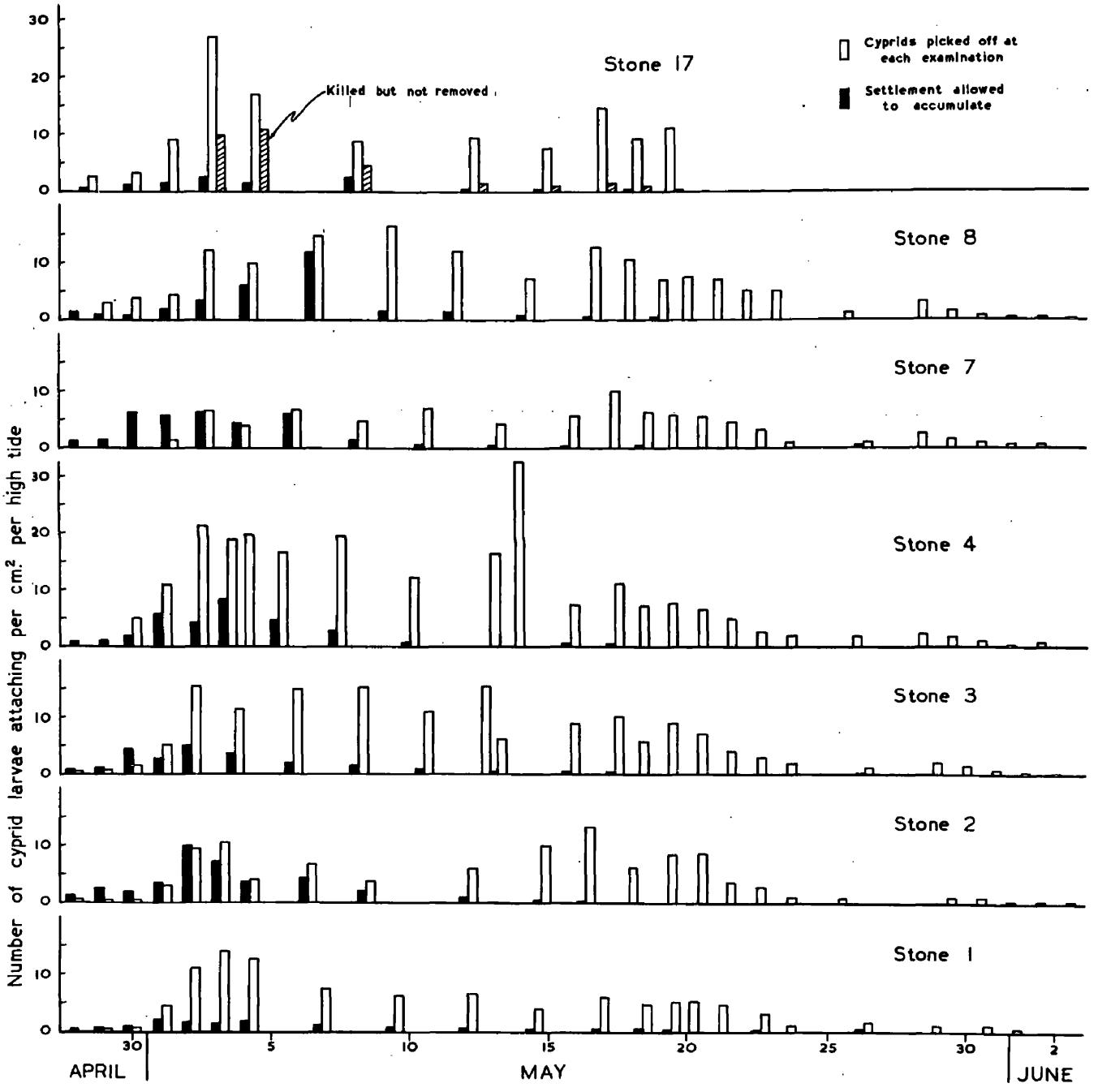
The daily increments during 1954 are given in Figure 2; also shown are counts made on an area of four cm.^{2} of each stone cleared at each examination by picking off the cyprids with a needle.

This settlement pattern could result either from variations in the planktonic larval supply or from changes on the rock surface as the settlement increases. The gradual increase to a maximum rate of settlement might be expected to result from individual variation in development of planktonic larvae and the wide dispersal of a single spawning. The counts made on the area cleaned daily on each stone, given in Figure 2, show a gradual increase in the number of cyprids settling from the plankton. Pyefinch (1948) found the same gradual increase in the number of cyprids in plankton samples at Millport.

Another explanation, independent of the plankton supply, has been suggested by Knight-Jones and Crisp (1953). They point out that if previously settled cyprids attract others to settle, the rate of settlement would be proportional to the numbers already settled. This would cause a logarithmic increase of the settled population similar to the early population growth of dividing flagellates in laboratory cultures. The authors stated that they have repeatedly witnessed this process, al-

Figure 2. Numbers of cyprids attaching per cm.^{2} per high tide during the 1954 settlement season. The black bars indicate the number of cyprids where they were allowed to accumulate, while the white bars indicate the numbers settling on adjacent areas on each stone where space was provided by picking off the cyprids with a needle at each examination.

On Stone 17, an additional area was modified by killing the cyprids and barnacles, but leaving them attached. Each pair of bars has been placed in the middle of the interval to which they refer.


Stone 17
Killed but not removed
Cyprids picked off at each examination
Settlement allowed to accumulate
Stone 8
Stone 7
Stone 4
Stone 3
Stone 2
Stone 1
Number of cyprid larvae attaching per cm² per high tide
0
10
20
30
30
5
10
15
20
25
30
2
APRIL
MAY
JUNE

though no data were given. To test this hypothesis, it would be necessary to eliminate the effect of an increasing planktonic larval supply, such as occurred in this study. In addition, if logarithmic growth is occurring, a semi-logarithmic graph of the data of Figure 1 should produce a straight line for the increasing portion of the curve. The data for 1954 were plotted in this manner and a distinct break in the curve occurred about May 1, when the rate of settlement increased markedly. This was evidently due to a sudden increase in the supply of larvae.

Gradual decrease in the rate of settlement would be expected to occur as the supply of larvae from a single main spawning dwindled. A decrease in numbers attaching to the cleaned area did occur in the second week of May, 1954 (Figure 2). However, the decrease on the natural area where the barnacles had been accumulating occurred in the first week of May, 1954 and a later increase in larval supply resulted in few attachments on the crowded area. Earlier indications of the avoidance by cyprids of crowded surfaces were observed in 1953. In this year, stone 1 received very few new settlers after April 20, but stones 7 and 8,

placed out on April 23, received a heavy set (Figure 1). The clearing experiment was repeated on all the stones in 1955 with similar results to those shown in Figure 2. It therefore appears that while the gradual increase in the settlement curves of Figure 1 was due to variations in the supply of planktonic larvae, the decrease was independent of this, being a function of the density of occupation on the surface of the stone.

Chipperfield (1948) counted the accumulating settlement of Balanus balanoides on pier piles at Liverpool, and also on Pecten shells exposed at intervals to study the variations in intensity of settlement. These counts show that after the settlement had stopped at all levels on the piles it continued on unoccupied shells placed out later. A similar accumulation of Bacteria and Protista on plates exposed to the sea is given on page 42 of Marine Fouling and its Prevention, (1952). Other examples of laboratory and natural populations undergoing sigmoid growth are given in Allee et al (1949).

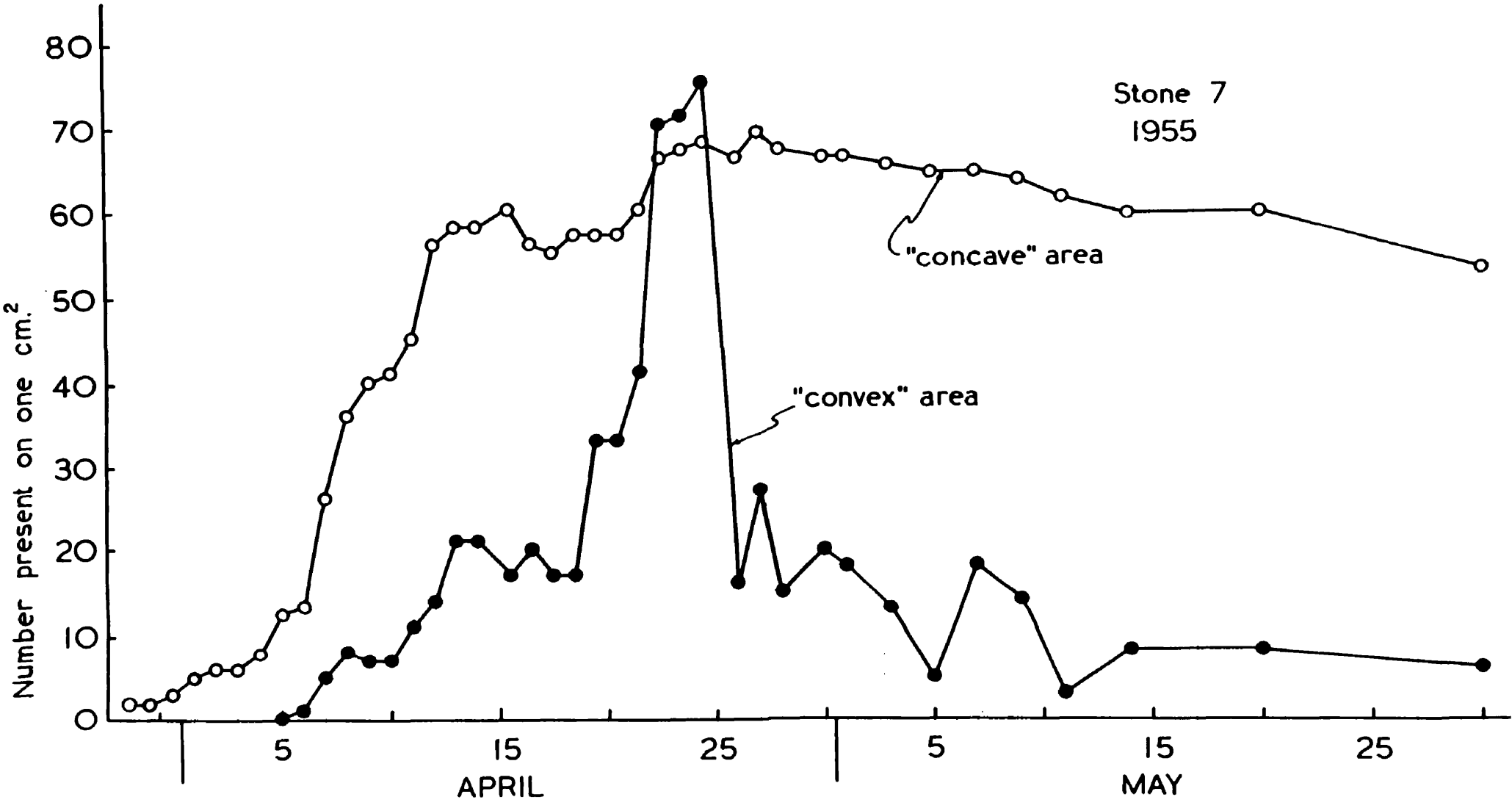
3. Observations on the behaviour of attaching cyprids.

The first cyprids attached in the hollows

and concave portions of the surface. An analysis of two small portions of Stone 7 in the 1955 settlement season is given in Figure 3. The settlement began earlier in the concave portion and in the first main wave of cyprids it became almost fully occupied. On the convex portion the settlement became dense only during the second increase in planktonic cyprids. The cyprids evidently attach to convexities only after the hollows are filled. This preference of cyprids for grooves and depressions in the surface has been often noted in literature on barnacles andCrisp and Barnes (1954) have described it in detail.

Some information was gathered concerning the amount of space needed by a cyprid to effect settlement and the reasons for avoiding densely occupied surfaces. It was noted frequently in the plotted areas that at high densities the loss of an individual was usually followed by an attachment in the same spot, usually by the next examination. The searching cyprid may have been attracted by some substance left behind by the damaged individual, or may have detected the open space on the otherwise occupied surface. Underwater, a densely occupied area is covered by a mass of beating cirri which probably makes searching rather difficult.

Figure 3. The accumulation of barnacles on two small areas about 5 cm. apart on Stone 7 in 1955. The concave area was a hollow one adjacent to some adults; the convex one was on a smooth raised area.


Stone 7
1955
"concave" area
"convex" area
Number present on one cm.²
0
10
20
30
40
50
60
70
80
5
15
25
APRIL
5
15
25
MAY

To get more evidence, a third area was established on stone 17, in addition to the two areas treated as on the other stones. The cyprids on this area were killed with a needle at each examination, but not removed. The cement usually holds dead cyprids and barnacles in place for some time. Some barnacles metamorphosed between examinations and these were also killed but not removed. Thus on this area there were damaged individuals, but there was no cirral beating or space, after a short time. As can be seen in Figure 2 the cyprids avoided this area after it became occupied.

It appears that a bare space on a suitable surface, even though it is only the size of a newly metamorphosed barnacle, is the only requirement for a cyprid disposed to attach. Prompt replacement of a missing individual in dense settlements of living barnacles indicates that the surface must be constantly searched, despite cirral activity.

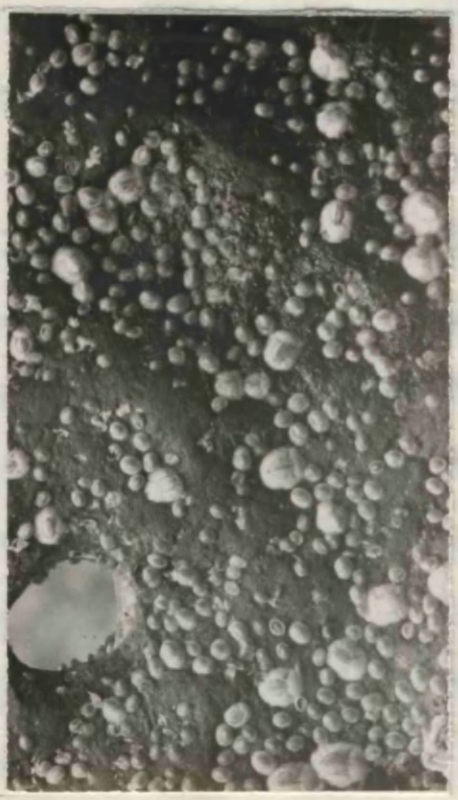
The numbers attaching to the cleared areas cannot be compared to those attaching to bare surfaces newly exposed, such as panels or shells, since some traces of the attachment cement and body fluids are inevitably left behind on the former. For the purposes of indi-

cating the presence of available cyprids and the variations in their abundance, however, comparison between cleared areas is probably valid.

4. Variations in settlement.

As can be seen from Figure 1, the time of the main settlement varied annually, although some cyprids settled in the first week of April in all three years. This agrees substantially with the other records for Millport of Elmhirst (1923), Pyefinch (1948) and Barnes and Powell (1953), the latest start being April 14. There were great annual variations in the maximum density reached on each stone. This density is the resultant of settlement and mortality. In the discussion of early mortality it will be shown that barnacles on any raised convex parts of the stones suffer heavy mortality; these places are usually bare at the end of the settlement season. If the portion of the stone which was being studied contained these convex places, the average density would be low even though the surviving barnacles were crowded together in the concavities. The photographs in Figure 4 illustrate this. If the concave areas had been considered separately the densities would probably have been very similar. The fact that

Figure 4. Photographs of stones 1 and 2 near the end of the 1954 settlement seasons and after some growth had taken place.



Stone
1.

May 14, 1954

July 9, 1954

Stone
2.

different portions of each stone were examined each year accounts for most of the differences in average density.

In section V, table 5.1, it is shown that the annual variations in density of settlement are of less consequence than the mortality after settlement in determining the relative strength of the various year classes. In his study of the planktonic stages of barnacles at Millport, Pyefinch (1948) found great annual variation in numbers of nauplii and cyprids in four years. His tables 8 and 9 indicate that in 1946 the survival from the nauplii to the cyprid stages was much lower than in the other three years. He has little quantitative data on the relation between numbers in the plankton and subsequent settlement. However, a comparison of his tables 3, 8 and 9, suggests an interesting situation. In 1945 the number of planktonic larvae was about 1/10 that of in 1944. Yet the density of newly settled cyprids in 1945 was 74/cm^2, as dense as any recorded in the present study (Figure 1). Later counts in 1944 and 1945 indicate that the density of young barnacles in 1945 was about 75 percent of that in 1944. These figures suggest that the settlement density is relatively independent of the supply of larvae in the plankton, as has been shown in this study. There may well be exceptions to this, however,

since Pyefinch points out that the poor survival of larvae in 1946 was followed by a poor settlement over a considerable area.

Some very interesting differences in settlement between adjacent shore levels were observed in 1954. On May 3, 1954, when the density of settlement on some of the stones had reached 35 per cm^2, it was noticed that bare boulders between MTL and LWN had only a very few cyprids and no metamorphosed barnacles. This was so at and above HWN too, although a period of neap tides during the previous week may have allowed little time for settlement at high levels, despite some wave action. The absence of settlement on the bare boulders just above LWN cannot be ascribed to any tidal action, however, since they were uncovered each low tide. After May 3, settlement then began to increase on these boulders; the first metamorphosed individuals appeared on May 6 and by May 16 the densities were from 12 to 20 cm^2.

This settlement of the bare boulders occurred after the stones (Figure 1) and adjoining rock surfaces in the mid-littoral region had been densely occupied. During this later period other bare surfaces were also being colonized, such as the shells of Mytilus edulis,

Nucella lapillus, and even the larger brown and green algal fronds. The principal difference between the surfaces which had been colonized first, such as the experimental stones, and the ones last occupied, was that the former bore adult barnacles.

The low boulders had adults as well as newly settled barnacles on them when they were first examined in June, 1953. Then during the summer they developed "hummocks", as described by Barnes and Powell (1950), the barnacles growing very tall, and packed closely together. During the autumn and early winter all the barnacles were stripped off by wave action so that by April they had been bare for 3-4 months. Nearer mid-tide level where growth is slower, the barnacles survived.

The most likely explanation for this delay in settlement on bare surfaces is one based on the work of Knight-Jones (1953a). He has conclusively shown that this species and other sessile animals are stimulated to settle by the presence of attached individuals of their own species. In the situation in this study, once the available space had been occupied in the zone where adults existed, the remaining cyprids in the plankton had to attach to any other unoccupied hard surfaces.

Barnes and Powell (1953) measured the settlement in 1951 on a series of intertidal panels attached to Keppel Pier, about one-half mile from the present study area. Their highest density was found just below MTL, and decreased irregularly above and below. They postulate that settlement is stimulated by the draining away of thin films of water, which are known to elicit a "clinging reaction". The suggestion implies that settlement follows the clinging reaction, although no direct observations of such a sequence were made. Barnes and Powell state that settlement would thus be stimulated in the zone between the high and low neap tide levels since the rise and fall of the tide would create such thin films. The decrease in density above mid-tide level is explained by an assumed increase in mortality with increased air exposure. This greater mortality has not been found in the present study. (See next section). Without direct evidence other than the original single series of panels, this hypothesis remains unsubstantiated. As pointed out by Crisp and Knight-Jones (1953), swarming at the surface and gregarious behaviour when settling would lead most of the cyprids of Balanus balanoides into the intertidal zone.

Other authors have observed the variation in settlement at different shore levels. Moore (1935) found the maximum densities varying from MTL to LWN, but mostly low on the shore. Hatton (1938) examined three localities for two years. In three instances the highest densities were at MTL (his level III) and in the other three at LWN (his level IV). In the second season when data on adult distribution are available all his levels had adults present.

Rice (1935), at Friday Harbour, Washington, counted the settlement of three barnacle species. Her results indicate that for Balanus cariosus, the number of adults was highest at MTL, as was the settlement. Balanus glandula, with no adults present, settled rather evenly, with slightly more at LWN. Chthamalus dalli, with only a few scattered adults, had equal densities at HWN and MTL and a lower density at LWN. From all this evidence it appears that settlement at various levels is related more consistently to the presence of adults than to any effect of tide.

5. Evidence of the sources of cyprid populations.

At any one point on the shore the settling population may have originated from several sources. The

Table 2.1 The relation of the state of the tide to the intensity of settlement.

Settlement season	Dates of intense settlement	Stone No.	State of tide
1953	April 12 - 16	1	Springs
"	April 20 - 27	7 & 8	Neaps
1954	April 4 - 6	1 to 8	Springs
"	April 11 - 13	"	Neaps
"	May 1 - 8	"	Last half of springs
"	May 13 - 20	"	Neaps to Springs
1955	April 6 - 13	"	Last half of Springs
"	April 18 - 24	"	Neaps to Springs
"	April 27 - 30	"	Springs to Neaps

Note: The periods of intense settlement were those which were relatively more intense than the settlements before and after.

following evidence indicates that on the study area the settlement was recruited from cyprid populations from successive spawnings.

a. Variation in the intensity of settlement.

Since the same small area on each stone was cleared and counted at each examination during the 1954 and 1955 seasons, these counts should give a true estimate of any variations in settlement. As can be seen in Figure 1, a small settlement occurred in early April 1954, followed by a week of no attachments and then by the main settlement in late April. Figure 2 gives the results of counts on the cleared areas in May and June. The heavy set which colonized the stones is followed by a slackening and later a slight increase.

The 1955 examinations were made more regularly and two heavy settlement periods and a possible third one occurred. Each peak in the three years studied has been compared to the state of the tide in Table 2.1. There does not seem to be any correlation between periods of heavy set and the state of the tide. Chipperfield (1948) exposed Pecten shells at intervals. He found three peaks of settlement, spaced 16 and 12 days apart, two at spring tides, one at neaps. Pyefinch (1948) studied the variations in numbers of planktonic larvae.

The plankton net was fished from a pier for an hour each day in a tidal current. This method is not quantitative, since the volume of water filtered may vary with the speed of the current. However,to indicate the relative abundance of naupliar stages in any one sample, this makes no difference, since it is unlikely that different stages are collected selectively. For each separate naupliar stage three distinct peaks of abundance were found, spaced 15 to 18 days apart. This could only result from three spawnings spaced at slightly more than two week intervals.

b. Differences in the size of settlers as the settlement season progressed.

During the second week of the settlement in 1954 it was noticed that the cyprids were markedly larger than those of the previous week. On April 13 all the individuals which had metamorphosed were measured with an eyepiece micrometer in a dissecting microscope. There had been little growth so that this probably represents the size of the individuals when newly metamorphosed. More measurements were made of those individuals which attached during the first four days after the renewal of settlement in the fourth week. The frequency distribution of these measurements is given in

Table 2.2

The relation of size of cyprid to the size of the barnacle into which it developed. (April 11-15, 1954 only)

Size range of cyprids in each group (mm.)	.70-.79	.80-.89	.90-.99	1.00-1.09	1.10 1.19	1.20 1.29
Number of individuals	1	10	13	37	43	11
Average length of cyprids	0.72	0.86	0.98	1.07	1.13	1.22
Average length of the barnacles developing from these cyprids	0.56	0.72	0.84	0.99	1.11	1.14
Length ratio, Barnacle/Cyprid	0.78	0.84	0.85	0.93	0.97	0.93

Figure 5. It can be seen that a population of small individuals began to settle in the first week and continued into the second week. A short heavier settlement of large individuals occurred in the second week. Then after a week's pause another settlement began, composed of almost all large individuals.

The differences in the measurements in Figure 5 are somewhat exaggerated, for the following reason. During the second week measurements were made on each individual cyprid and then on the same barnacle which metamorphosed from it. The cyprid measurements were grouped into 1/10 millimetre classes, and the average size of both cyprids and metamorphosed barnacles in each cyprid size class was calculated. These data are given in Table 2.2. Cyprids less than 1.0 millimetres in length developed into relatively smaller barnacles than the larger cyprids. These smaller cyprids were of a darker colour and the dorsal edge of the carapace was more sharply ridged; the larger cyprids were more rounded dorsally and of a lighter colour.

The reason for the small size of this first group of settlers is not known. They may either have originated from a different spawning stock or perhaps had less favourable circumstances during their early planktonic life. Their survival was much poorer than the larger

Figure 5. Measurements of newly metamorphosed barnacles in the first, second and fourth weeks of the 1954 settlement season. The measurements in each week refer only to barnacles attaching during that week.

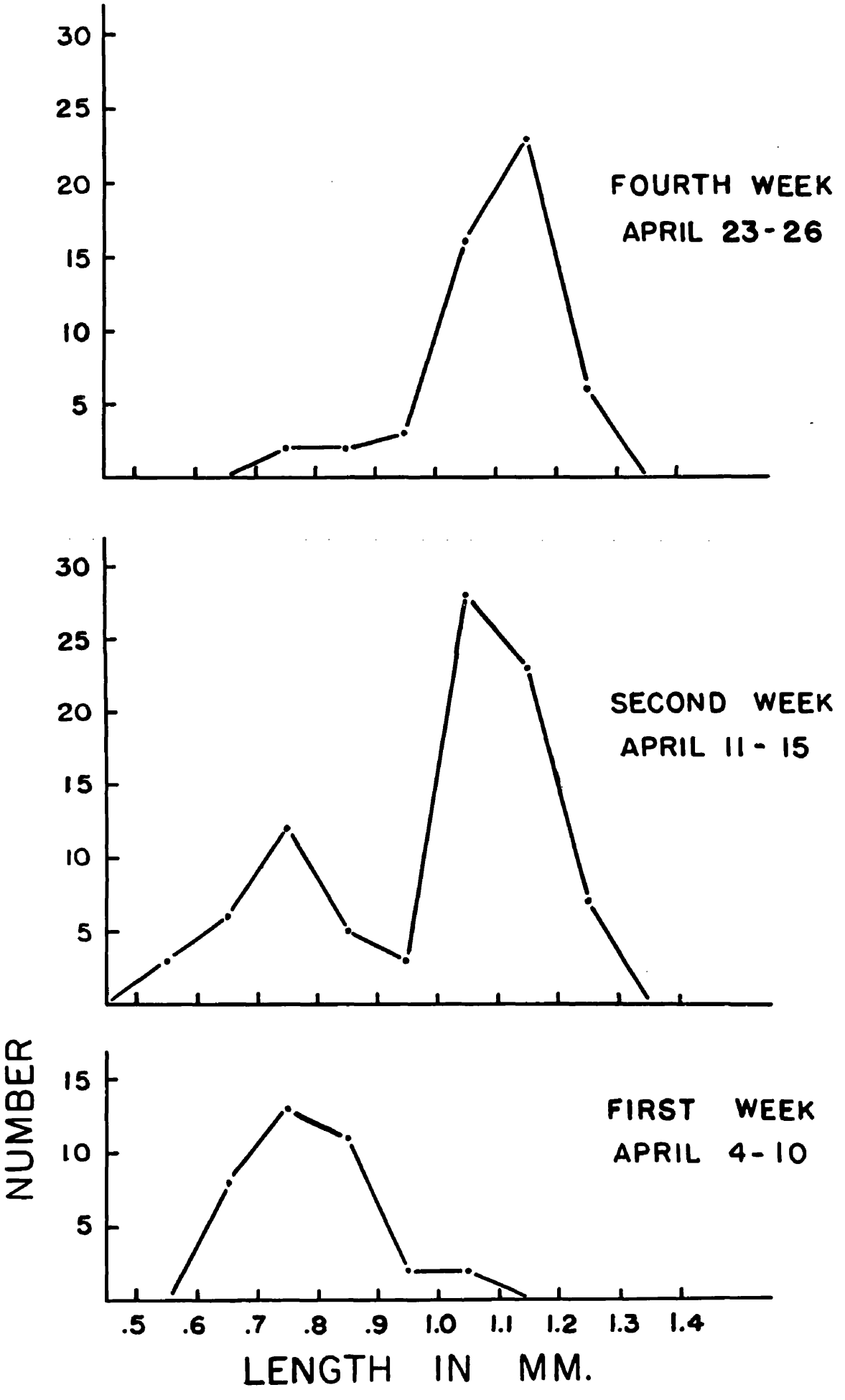

30
25
20
15
10
5
FOURTH WEEK
APRIL 23-26
30
25
20
15
10
5
SECOND WEEK
APRIL 11-15
NUMBER
15
10
5
FIRST WEEK
APRIL 4-10
.5
.6
.7
.8
.9
1.0
1.1
1.2
1.3
1.4
LENGTH IN MM.

Table 2.3 Length of cyprids of *Balanus balanoides* in various localities.

Locality	Average length, mm.	Size range, mm.	Authority
Herdla, Norway	1.20	---	Runnstrom, 1925
Altane Fjord, Sweden	---	1.02 - 1.24	Barnes, 1953a.
Plymouth, England	0.94	---	Bassindale, 1936
Liverpool, England	1.09	0.90 - 1.25	Chipperfield, 1948
Millport, Scotland	---	0.84 - 1.20	Barnes, 1953a.
" "	---	0.90 - 1.10	Pyefinch, 1948
Present study, attached cyprids:			
Millport, Scotland	1.05	0.72 - 1.21	Second week, 1954
Millport, Scotland	1.13	0.97 - 1.25	Fourth week, 1954

individuals attaching in the second week. (See section III). The possibility that they were cyprids of another species was disproved by later examination of the ones which survived and grew. It appears that the settlement in the first two weeks of the 1954 season came from two sources.

These cyprid measurements were made on attached individuals; as pointed out earlier, these have the anterior end pulled down, so that for comparison with measurements of planktonic cyprids the sizes may be slightly smaller. Measurements of planktonic cyprids by other workers are given in Table 2.3. Some of the cyprids in the fourth week, 1954, were larger than those measured at Millport previously.

Barnes (1953a) measured Balanus balanoides cyprids in a series of five plankton hauls made over two and one-half weeks at Millport. He found two modal sizes, one at 1.02mm, the other at 1.12mm. Both modes persisted for the period studied; this was interpreted as indicating the presence of two populations in the plankton. He also measured stage I nauplii teased out of barnacles in the laboratory. Nauplii from one-year-old barnacles taken from low in the intertidal zone were slightly smaller than those from barnacles of twice their length

collected from a high zone. No test of significance of the small difference between these average naupliar sizes was made, however, and the effect of adult size and different shore level cannot be distinguished. Barnes suggests from these data that the different sized cyprids have originated from different levels on the shore.

c. Variations in the time necessary to metamorphose after attachment.

The dates of both initial attachment and subsequent metamorphosis were recorded for all the individuals plotted on the stones. Calculations of the average time between attachment and metamorphosis for the cyprids attaching each day were made in the hope of revealing any effects of tidal level or season on the cyprids.

Only those periods when daily examinations were being made were chosen for the calculation. Any cyprids which metamorphosed the day following the date of recorded attachment were recorded as taking one day to metamorphose. This is the best possible estimate since they had had two high tides to attach before they were recorded and two in which to metamorphose by the next examination. Metamorphosis the second day was recorded as two days and so on. The total number of days to metamorphosis was divided by the number in each day's settle-

Table 2.4 The average time taken by cyprids to metamorphose after initial attachment during periods of high and low intensity of settlement.

Dates of attachment	Intensity of set	Number of individuals observed to have metamorphosed in each of the days following attachment				Total No. individuals	Average no. of Days
		1 day	2 days	3 days	4 days		
1953, Stone 1. only.							
Apr. 11-12	Light set	9	14	2	--	25	1.7
Apr. 13-16	Heavy set	301	67	7	--	375	1.2
1955, Stones 7 and 8 together							
Mar. 28-Apr 6	Light	40	136	25	7	209	2.0
Apr. 7 - 13	Heavy	208	208	17	5	438	1.6
Apr. 15 - 18	Light	15	8	2	3	28	1.8
Apr. 19 - 24	Heavy	122	70	4	0	196	1.4
Apr. 26	Light	9	3	0	2	14	1.6
Apr. 27 - 30	Heavy	55	8	3	1	67	1.2

Note: The intensity of set in 1955 was determined from counts made on areas cleaned daily. A heavy set was defined arbitrarily as consisting of more than 10/cm.^{2}/ tide.

ment which survived to metamorphose. This gave the average metamorphosis time for each daily settlement. This, of course, is an estimate based on examinations made only once a day and so is useful only for comparative purposes. The true time between attachment and metamorphosis would probably be somewhat shorter than that calculated.

The longest series of daily observations took place in 1955 on stones 7 and 8. The settlement intensity was judged from the numbers attaching to the area which was cleared at each daily examination on these stones. The 1955 settlement season was characterized by three periods of low settlement rate, (less than 10 cyprids/cm^2/ two high tides), each followed by a period of higher settlement rate. All the cyprids which attached and metamorphosed in each period were taken and the average time between attachment and metamorphosis calculated. These data are given in Table 2.4 and it can be seen that at the times of low rate of settlement the period between attachment and metamorphosis was longer. The records of stone 1 in 1953 were treated similarly, since daily examinations had been made then in periods of both low and high settlement rates. Similar variations occurred in both years.

One possible explanation for this is suggested by the work of Knight-Jones (1953b). He has shown that artificial prolongation of the planktonic life of Spirorbis borealis leads to profound changes in the behaviour of the larvae. They show much less discrimination in their choice of settling surface after a longer swimming period. The similarity in the mode of life of the adults and in the gregarious behaviour when settling of the larvae of Spirorbis and Balanus, lends support to the assumption that similar physiological changes may occur in the Balanus planktonic larvae. Chipperfield (1948) noted that cyprids which had been brought into the laboratory settled in from one to four days. He believed that this variation might indicate that a cyprid needed to develop a certain physiological condition before it attached. Knight-Jones (1953a), prolonged the swimming stage of Balanus balanoides cyprids in the laboratory for two weeks with little ill effect. His numbers were too small, however, to determine whether they attached more readily after this delay. Pyefinch and Mott (1948) noted variations in the sensitivity to copper of cyprids caught on different days. Near the end of the settlement season, with the decrease in numbers of cyprids caught, the sensitivity increased. In addition, the sensitivity of cyprids kept in the laboratory increased the

the longer they were kept. Some of each batch caught were kept as controls; the time taken by the controls to attach after being caught was shorter in the groups which exhibited high sensitivity. This evidence seems to indicate that the cyprids undergo physiological changes in the plankton.

If planktonic cyprids go through physiological changes which lead toward their eventual settlement and metamorphosis it might be expected that the longer they remained in the plankton, the more ready they would be to settle and metamorphose, as Knight-Jones showed with Spirorbis. If this is so, the observed lengthening of metamorphosis time between the peaks in settlement intensity may be evidence that a different population is beginning to arrive, composed of cyprids spawned later than those which composed the preceding peak in settlement. The first arrivals of a later spawning would have been in the plankton a shorter time than the last settlers of the previous spawning and would take longer to metamorphose after attachment.

Another possible explanation is that the metamorphosis might be hastened at a time of heavy settlement by some stimulus to the attached cyprids such as an increase in the number of contacts with searching

cyprids. This seems less likely, but a controlled experiment would be needed to decide this question.

To sum up, the evidence of successive increases in the rate of settlement, the presence of separate size groups of cyprids and the regular decrease in the period between settlement and metamorphosis for each peak of settlement all seem to indicate that the shore population is derived from successive spawnings.

Whether these spawnings come from separate locations or whether only part of the population at any one place spawns at once is not known. Examination of the reproductive condition of adults of Balanus balanoides by Pyefinch (1948) and Bousfield (1954) in early spring indicated that some individuals of a population may spawn earlier than others.

Moore (1934) noted a separate late settlement of Balanus balanoides at Port Erin in 1931. Chipperfield (1948) observed variations in intensity of settlement of Balanus balanoides on shells exposed at intervals. Pyefinch (1948) and Barnes and Powell (1953) working with Balanus crenatus have shown that successive settlements take place throughout the summer. Crisp and Davies (1955) showed that in Elminius modestus, the same individual may spawn more than once during the summer,

Table 2.5. The relation of the average time between attachment and metamorphosis to height on the shore. April 4-29, 1954

Stone numbers	Vertical Distance in Feet from MTL	Number of Individuals	Average time between attachment and metamorphosis in days.
7 & 8	+ 2.0	193	1.64
3 & 4	+ 0.9	267	1.41
1 & 2	-1.0	225	1.74

Note: These average times, although computed from identical observations on all the stones, cannot be compared with those in Table 2.4, since some longer intervals occurred between examinations in 1954.

rapidly refilling the ovaries with new eggs while the embryos of the previous fertilization were developing. There is no evidence for such a process in Balanus balanoides; refilling of the ovaries occurs slowly during the summer, fertilization only in the autumn.

During the 1954 settlement season the length of time between the examinations of the stones varied. For this reason it is impossible to compare the average time between attachment and metamorphosis in 1954 with the other years. However, from April 4 to April 29 the examinations were made on the same days on all the stones, so that the data are strictly comparable between shore levels. For this period all the barnacles attaching on each pair of stones at the same level were taken as a group, and an average time between attachment and metamorphosis calculated. These calculations are given in Table 2.5. It appears from these data that longer immersion has no consistent effect on the period between attachment and metamorphosis.

These studies of three settlement seasons at Millport have shown that the supply of larvae in the plankton has always been more than adequate to populate the favourable places. The survival of these settlers will be considered next.

III Mortality during the settlement season.

The main portion of this study has been devoted to following the survival of barnacles under various natural and experimental situations. The remainder of this paper is divided into parts corresponding approximately to successive periods in the life of a barnacle. These divisions are:

1. The settlement season before any appreciable crowding takes place.

2. The succeeding growing seasons when crowding seems to be of great importance.

3. The mortality at high shore levels where no crowding or predation occur.

4. The period of predation by Nucella lapillus.

1. Daily mortality in relation to the weather changes.

Since observations were closely spaced during the settlement season it seemed advisable to calculate the percentage of deaths which took place between observations and study this in relation to the daily weather changes. It was found that if more than one day had elapsed between examinations, it was often difficult to connect the mortality with the weather, which often showed sharp

changes from day to day. Observations each day had been made only during the 1955 season, so that for this particular analysis, these data alone were used. For each daily interval the number which died was divided by the average number present.

A dead barnacle can be recognized by the appearance of its shell which becomes shrunken and discolored in patches in very young individuals and chalky white in older ones. Also, the opercular valves are often sunken or gaping open. The time of death of cyprids was much more difficult to determine since they often remained cemented in position for a week or more before falling off. These gradually became withered and dark, but no criterion was found, other than disappearance, for assigning an exact date of death. For the cyprids, therefore, it was decided to take each day's attachments as a group, calculate the percentage which never metamorphosed, and consider this mortality with reference to the weather of the day following attachment. This calculation assumes that most deaths were caused soon after initial attachment, which is probable. Only data for those days on which ten or more cyprids attached were used; this limited the comparison to the fairly short period of heavy settlement.

Table 3.1 -- The mortality per day of cyprids and barnacles during the 1955 settlement season in relation to the daily weather.

Daily Weather	Average percentage death per day of metamorphosed barnacles		Fraction of the total days in each weather type when the mortality exceeded a specified percentage.			
			Metamorphosed barnacles, mortality greater than 5% per day.		Cyprids	
					Mortality greater than 20% per day	Mortality greater than 10% per day
	Stone 7	Stone 8	Stone 7	Stone 8	Stone 7	Stone 8
Warm, calm	2.4	0.7	0/5	0/5	4/4	3/3
Warm, light wind	1.2	0.3	0/3	0/3	1/1	0/1
Cold, sunny, windy	4.0	1.7	1/8	1/8	2/2	---
Partly cloudy	3.6	1.4	3/13	0/13	4/8	3/4
Rain (over 0.05 in)	2.5	2.1	1/10	1/10	3/6	3/4
Gale	16.4	7.1	1/2	1/2	1/1	---

From daily observations of the weather, supplemented by the temperature, rainfall and wind records made at the laboratory, six weather classifications were made; these are given in Table 3.1. The daily intervals between examinations were grouped under their appropriate weather type and the average daily mortality rate for each type was calculated as indicated above. The other columns of the table indicate, for each weather type, the occurrences of exceptionally great mortality, shown as the ratio of the number of days of high mortality to the total number of days. For the metamorphosed barnacles the days listed are those when the mortality exceeded 5% of the total number present during the interval. For the cyprids, where the average mortality, especially on stone 7, was much greater, the days listed are those when the mortality exceeded 20% on stone 7, and 10% on stone 8.

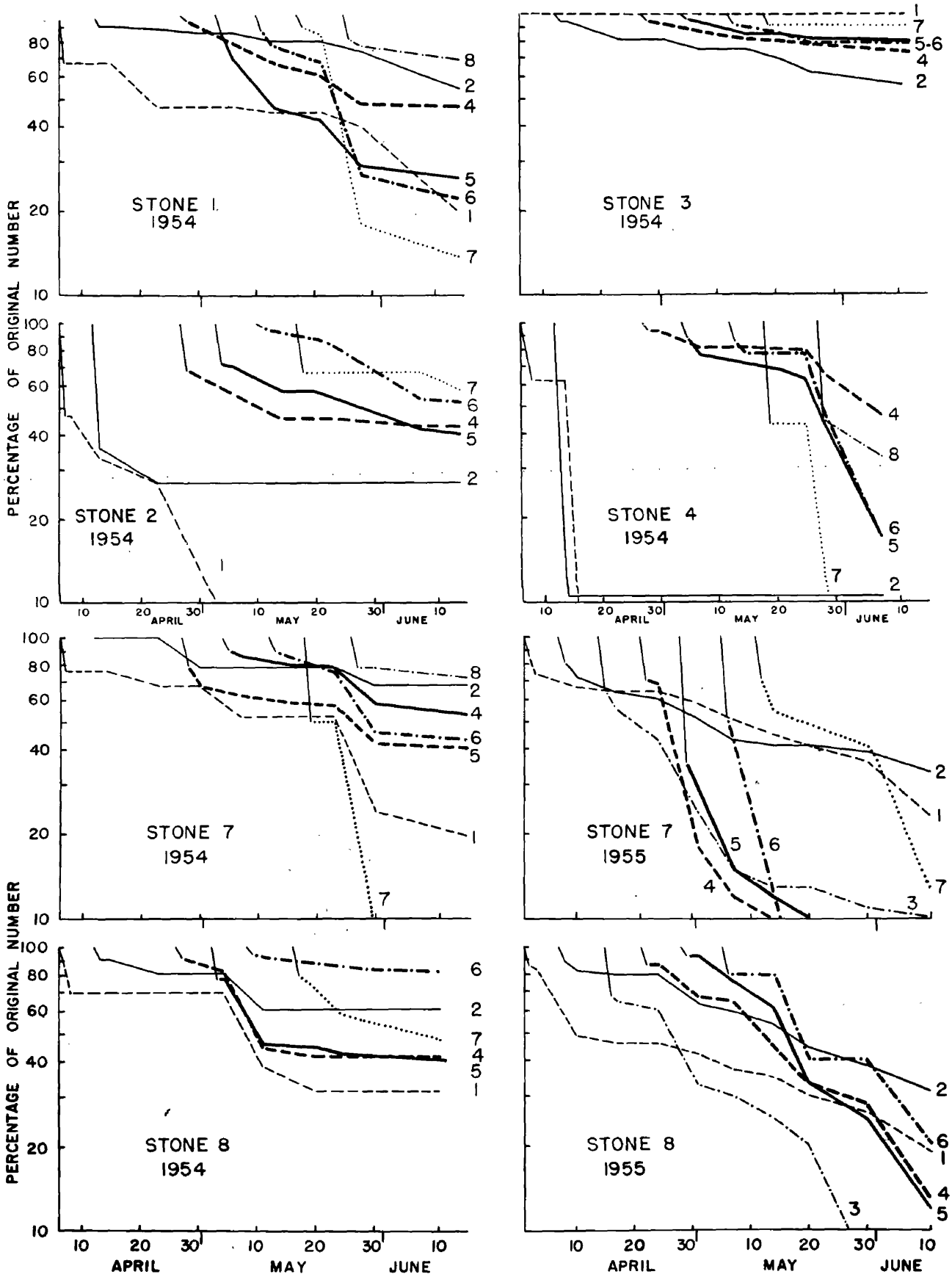
From this table it can be seen that cyprids attaching during the five continuous very warm days suffered more mortality than those experiencing cloudy or rainy weather shortly after attachment. On the other hand, warm days were associated with only average mortality among metamorphosed barnacles, but windy days and especially gales caused great damage.

2. Differential survival of early and late settlers.

Another analysis of the data was carried out as follows. Taking each stone separately, the individuals which had attached in each week of the settlement season were taken as a group and their survival curve was plotted. These curves for 1954 and 1955 are shown in Figure 6. Since it has been assumed that any cyprids which failed to metamorphose died within one day after attaching, the cyprid mortality for each week was combined and plotted as occurring in one day.

It can be seen that no general relation exists between cyprid mortality and time of attachment, cyprids attaching in some of the later weeks surviving better than in earlier ones, and vice versa. Since later setlers must generally attach to more densely occupied surfaces, the same lack of correlation seems to exist between higher density and greater mortality. In 1954, the main settlement occurred in weeks 5 and 6 (Figure 1); a comparison of the cyprid mortality in weeks 4, 5, and 6 shows that on stones 1, 3, and 4, the death increased with increasing density of set, on stones 7 and 8, it decreased, and on stone 2, it increased and then decreased. At the end of settlement, during weeks 7 and

Figure 6. The survival of Balanus balanoides from initial attachment as cyprids during the 1954 and 1955 settlement seasons. All the cyprids which attached in each week of the season were taken together and their survival plotted as the percentage of the original number. The beginning of each curve, shown as a thin continuous line, indicates the percentage of cyprids which died before metamorphosis; this cyprid mortality was assumed to have happened within one day after attachment, and this portion of the curve was plotted accordingly. The rest of each curve is the survival of metamorphosed barnacles, the points being at weekly intervals to allow easier comparison between the slopes of the curves. The slope indicates the relative death rate, since the ordinate is on a logarithmic scale. See text for further explanation.


STONE 1
1954
STONE 3
1954
STONE 2
1954
STONE 4
1954
STONE 7
1954
STONE 7
1955
STONE 8
1954
STONE 8
1955
PERCENTAGE OF ORIGINAL NUMBER
APRIL
MAY
JUNE

8, the mortality usually, but not always, increased. Similar irregularities occurred on stones 7 and 8 in 1955.

The high cyprid mortality during the third week of the 1955 season can be ascribed to the unusually warm calm weather at this time. During 1954, a comparison of stones 1 and 3, protected from the direct sun, with the unprotected stones 2 and 4, shows the damaging effect of the sun. Only on stone 3 in 1954, protected from the sun and most wave damage, did the mortality of cyprids increase from the first to the fifth week. Thus with the main environmental causes of death removed there seems to be better survival among earlier settling cyprids on Stone 3.

The survival of the metamorphosed barnacles in the various weekly sets can be compared best by considering the death rate over a short period of time when considerable mortality has occurred. Without some destruction no selection between weeks can be occurring, as is shown on stone 3, while to make a comparison of the percentages surviving at the end of settlement would ignore the fact that the earlier weeks' settlements have been exposed to death longer. Since the relative death rate is indicated by the slope of the curve, the mortality can be easily compared in any chosen interval.

It has been shown that the individuals in the first week of the 1954 season were small, and in general their survival was very poor. The rest of the settlement seemed to be composed of normal-sized individuals so that for the purpose of this discussion only weeks 2 to 8 will be considered. The greatest mortality in 1954 occurred on stones 1, 2, 4, and 7, during a gale on May 25th. A comparison of the curves of weeks 2 to 7 (the settlement of week 8 followed the gale) shows that the earlier sets survived better than the later ones, as indicated by the increasing slopes of the curves of the later sets. This is true in 18 of the 20 curves (5 weeks on 4 stones); the two exceptions are week 7 on stone 2, and week 5 (which was equal to the previous week) on stone 7.

In 1955, a similar increase in mortality rate of later settlers occurred on stone 8 from May 14-20, though from April 24-30, there was a lower death in the fourth than in the third week. On both stones the sets of the first two weeks show a markedly better survival rate than all the later ones. The consistency of these results is surprisingly good, considering that these are natural populations exposed to accidental damage from

debris, etc. Early settlers, being older, have probably had more time to develop a thicker shell and a broader base; also, they had attached at a time when density was low and when there presumably was a better choice of attachment sites. As was pointed out in the previous section, during the early parts of the three settlement seasons observed in the present study, cyprids attached first in the pits and hollows of the irregular surfaces of these stones. Once these hollows were occupied, the later settlers had room to attach only on the unoccupied convexities of the surface. As was shown in Table 3,1, warm weather caused no great mortality to metamorphosed individuals, most death being associated with windy days and gales when damage by waves or wave-borne objects is likely. It might be supposed that barnacles on the higher portions of the surface would be more likely to be damaged than those in hollows. To test this, two small portions of the area studied on stone 7 in 1955 were chosen, one a concave area where barnacles had persisted, the other a convex one which was almost completely bare at the end of settlement. From the individual records the curves of settlement were constructed and are shown in Figure 3. The settlement started a week later on the convex area and during the main settle-

Table 3.2 -- The mortality during the settlement season in one gale on April 25, 1955. The barnacles attaching during each week of the season before the gale are treated separately, to indicate the effect of age; two types of surface were considered separately also.

Type of surface	Concave				Convex		
Week of settlement season :	1	2	3	4	2	3	4
No. alive April 24:	8	23	15	13	8	5	56
No. dying between April 24 and 26 :	0	0	1	1	5	3	51
% death in the interval :	0	0	7	8	62	60	92

ment period in early April only reached one-third the density of the concave area. An increase in planktonic cyprids about April 20, as indicated by increased attachments on an area of stone 7 cleared of cyprids daily, resulted in a rapid colonization of the convex area when the concave areas were almost completely occupied. The gale of April 25th caused great destruction on the convex area, but not on the concave one. The behaviour of cyprids leading them to attach in hollows evidently has great survival value.

This same analysis was used to determine whether the earlier sets survived better by virtue of their greater age, when presumably they would have a somewhat thicker shell. The two areas were divided into the weekly sets and the death rate during the April 25th gale calculated. These calculations are given in Table 3.2. A much greater difference is shown in the death rates between the two areas than in those within each area. There is some suggestion that within each area the earlier settlers can better withstand the effects of a gale. However the protection offered by the concavity is much more important, indicating that the earlier settlers survive better because they occupy the more protected positions.

3. Discussion of the causes of early mortality.

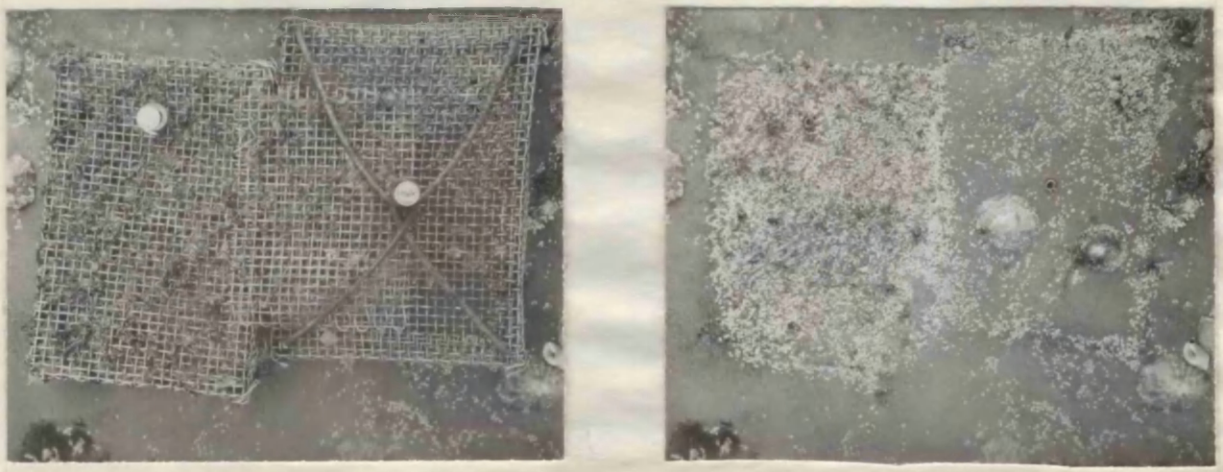
From the previous findings it appears that physical damage is the most important cause of early mortality, with some additional mortality of cyprids from exposure to the sun during hot weather. After gales, many barnacles were noted as missing, and some of the rest had wall plates broken or cracked. It seems probable that this damage was caused by wave-borne objects rather than by the force of water alone, but there is no evidence on this matter.

Another agent which may cause such damage is the limpet, Patella vulgata. In 1955, regular grooves were noted on the stones, as shown in Figure 7. Broken barnacles were found in association with these grooves, on some days when no appreciable wave action was occurring. The dimensions of these scratches are such that they could have been made by the radula of a limpet. An experiment performed during the 1954 settlement season to demonstrate the effect of limpets is illustrated in Fig. 7. Two cages were attached to a slope of bare rock where limpet radula marks indicated heavy grazing. One cage was attached over two limpets, the adjoining cage having none. After the settlement season was over, the photographs in Figure 7. were taken. It is possible

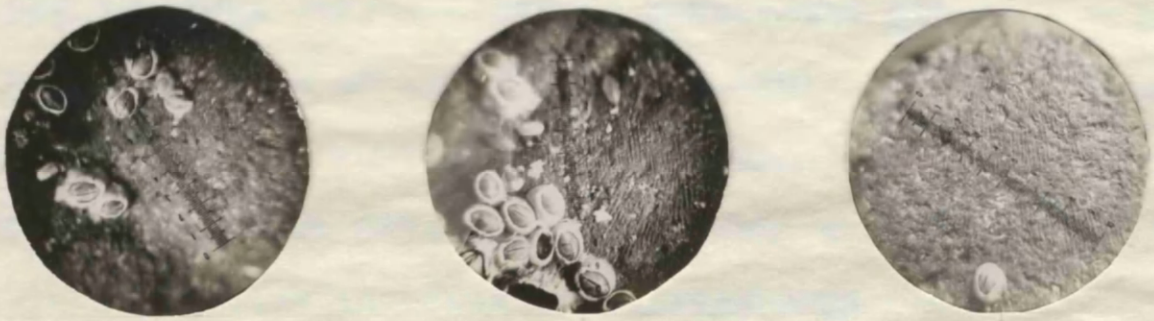
Figure 7. (a) The effect of grazing by Patella vulgata on newly settled barnacles. The cages had been in place during the 1954 settlement season; these photographs were taken on June 22 One cage enclosed two limpets, the other excluded all limpets (x 1/6)

(b) Photomicrographs of radula marks on Stone 7, May 5, 1955, presumably made by a limpet. (x3.4)

(c) A trap which caught fishes and crabs which visited the intertidal zone at high tide; it is about two feet long.



a.



b.

c.

Table 3.3 -- Percentage mortality during three successive settlement seasons.

Stone No.	Ht. from MTL in feet	Percentage of the total cyprids attaching which did not metamorphose	Percentage of those which metamorphosed but which died before the end of the settlement season	Percentage of all those which attached which died before the end of the settlement season.
		1953 settlement		
8	+ 2.2	13	11	22
7	"	18	23	37
4	+ 1.1	23	23	40
3	"	5	7	12
2	- 0.9	18	63	70
1	"	13	17	28
		1954 Settlement		
8	+ 2.2	8	22	28
7	"	13	43	51
4	+ 1.1	13	75	78
3	"	5	17	21
2	- 0.9	22	42	55
1	"	13	65	70
		1955 settlement		
8	+ 2.2	12	43	50
7	"	30	65	76

that the restriction by the cages may have resulted in more intense grazing inside the cage than on the open shore. But it seems obvious that the limpets can reduce the density of barnacle settlement appreciably. Inside the cages on Area 1 (described in the next section) the density of settlement in the narrow spaces between the tall older barnacles was very high. This suggests that the limpets present in the cages were not able to graze in these places. Hatton (1938) cleared the limpets away from the area surrounding his settlement sites to prevent the destruction of the young barnacles. He states that the limpets did not damage older barnacles; this was confirmed in the present study by the good survival of older barnacles in cages with limpets on Area 1.

The effect of increased exposure to air at higher shore levels is difficult to ascertain from these data, since the stones are not strictly comparable in surface roughness or angle of attachment. A summary of the overall settlement season mortality is given in Table 3.3. From this it can be seen that even on the stones most similar in situation, numbers 2 and 4, there was greater cyprid mortality on the higher one in 1953 and on the lower one in 1954. The mortality among the metamorphosed barnacles was the inverse of this. Also, the highest

pair of stones, numbers 7 and 8, never had the highest mortality. This lack of correlation with increasing air exposure would be expected from the evidence that wave damage rather than warm weather is the more important cause of death. Once metamorphosed, the most dangerous time for newly settled barnacles is when they are immersed.

Deevey (1947), using the data of Weiss (1948), suggested that survival was poorer at times of maximum settlement of Balanus improvisus on continually submerged glass plates in Florida. This data was obtained by comparing the final numbers of barnacles surviving on plates exposed for a month with the sum of the numbers of cyprids attaching each day to a plate wiped daily. At certain times, fewer attached over a month to the plate cleaned daily than survived after a month's exposure on the other plate. This suggests that the wiped plate was less attractive to cyprids than the one which had both a bacterial slime and previously settled barnacles, both of which have been shown to increase the numbers attaching. (Miller et al 1948, Knight-Jones 1953a). In addition, the maximum number on the panel exposed for a month depended not on the area but on the

season, since during the summer the faster growing barnacles covered the panel with about a third of the number that could attach in winter. Thus, from this study no accurate relation between mortality and density can be derived. In the present study it has been shown that the mortality of cyprids is not correlated with density. The increased mortality of those metamorphosed individuals which attached late in the season when the density of occupation of the surface was high has been shown to be due primarily to the previous occupation of protected sites.

There is a possibility that some of the early mortality may be due to predation by associated animal species. The effect of Patella vulgata has been discussed. As will be shown later, Nucella lapillus does not feed much on young barnacles if older barnacles are available as food. On the stones used, older barnacles were present, so that is is doubtful that Nucella caused much mortality to the newly settled individuals.

To investigate the other animals associated with the barnacles, all the organisms on small areas of barnacle covered rock were collected on several occasions in the summer and autumn of 1953. This material was brought into the laboratory and examined. Collections

were made from above and below MTL. The principal groups represented were the Turbellaria, Nematodes, Oligochaetes, Gastropods, Lamellibranchs, Ostracods, and Hydracarina. Fewer Copepods, Amphipods, Isopods and the insects Anurida maritima and Chironomid larvae were found, plus a few polychaetes of the species Eulalia viridis. Only the last species would be likely to be a possible predator. Moore and Kitching (1939) observed Eulalia opening a barnacle. Several observations of foraging by Eulalia were made in this study; the worms seemed to be searching in all the crevices and empty barnacles. One was seen capturing a large chironomid larva among barnacles, but no sign of any attack on live barnacles was observed.

To study the larger animals, a fish trap (see Figure 7) was constructed over an area of barnacles so that any fish or crabs foraging over the surface at high tide would be caught. No bait was used. Seven species of fish and three species of crabs were caught during operation of the trap for 19 tides in July and August, 1953. The list of species caught is as follows:

FISH	CRABS
Labrus bergylta	Portunus puber
Ctenolabrus rupestris	Carinas maenas
Centrolabrus exeoletus	Cancer pagurus

Gadus virens

Cottus bubalis

Onis mustela

Onis mediterraneus

Only Ctenolabrus rupestris was caught regularly.

A few stomachs of each were examined, and traces of barnacles were found only in those of Labrus and Portunus. No blennies, Blennius pholis, which have been stated to feed heavily on barnacles (Hartley, 1949) were caught.

The droppings of the Purple Sandpiper, Calidris maritima and the Black-headed gull, Larus ridibundus were examined but no barnacles were found in them. Rock pipits, Anthus spinoletta were common but the observations of Gibb (quoted in Lack, 1951) indicate that Littorina and Idotea are its principal food. Rats and rabbits were also observed on the shore but no stomach contents were examined.

From this superficial survey it would seem that none of these possible predators in their present abundance could cause mortalities among newly attached barnacles comparable with those associated with gales.

IV. Mortality from crowding.

A. Description of the study areas.

In November, 1952, the first area was established on a six foot vertical face of sandstone extending from mid-tide level to above the upper level of the distribution of Chthamalus stellatus. It formed the west side of one of the ravines. Most of the force of the waves from the sea to the south was thus exerted across this face rather than directly against it.

On this vertical area three horizontal levels were chosen, 20 centimetres distance apart, vertically. At each level the barnacles on three squares of about 25 to 30 cm^2 were mapped. The squares were about 10 centimetres apart horizontally. Then one of the squares at each level was covered by a cage, constructed of 1/8" mesh stainless steel wire netting; the cages were about 5 inches square and one inch high. The edges were fitted closely to the undulations of the rock to prevent any Nucella lapillus from entering. The space of an inch inside the cage above the barnacles and the rather wide mesh allowed what appeared to be an adequate opening for the passage of feeding currents. The specifications for this mesh as woven of No. 22 gauge wire, indicated an open screening area of 60.2%. Subsequent growth of indi-

viduals inside the cage appeared to be equal to that of those outside, and at the same density survival was about the same, another indication of similar growth.

In addition, a sheet of the same netting was spread out from one side of the cage over one of the adjoining census squares, about one inch away from the rock surface. This afforded protection to this square from damage by floating objects and provided somewhat similar conditions of current, wave and lighting as the cage while allowing Nucella free movement underneath. This square was termed the "cover", while the unmodified one was termed "control". The method of attachment of these cages was similar to that of the stones described in section III. A photograph of this area is given in Figure 19.

The mapping of each square was done on graph paper, a grid of threads of one square centimetre opening being used as a guide on the rock surface. In November 1952, every individual was mapped and the settlement of that year, then six months old, was distinguished from the rest. It was possible to distinguish these from the older year groups, by their smaller average size and the appearance of the shell. In barnacles aged 6 months above MTL, the shells were quite thin, and the upper edges of the parieties are still uneroded; the surface was fairly

Table 4.1 -- The overlap in size between the largest individuals of Balanus balanoides at six months of age and the smallest individuals at 18 months of age. All barnacles uncrowded.

Area	Dates of measurements	Length in mm at age six months		Length in mm at age eighteen mos.		Authority
		Average	Largest individual	Average	Smallest individual	
Upper Control 1	Nov. 5, 1954	2.2	3.4	3.8	3.4	Photographs of Area 1, present study
Upper Cover	"	2.4	3.6	3.8	3.0	
Middle Control 1	"	2.9	3.6	4.1	4.0	
Low Control 2	Nov. 14 1954	2.8	3.6	3.9	3.5	
Panel 3	October of 1951 and 1952	14.5	18.4	18.8	14.7	Original data of Barnes and Powell(1953)
Panel 5		16.0	18.5	20.5	16.8	
Panel 6		17.0	20.4	20.0	16.7	
Panel 7		17.5	19.4	21.5	14.6	

smooth and white. The previous year group, then aged 1½ years, had undergone much erosion so that the upper edges of the shell were thick and rounded, no new shell having been added there. (Growth in the compartments of a barnacle, according to Darwin (1854), occurs only along the basal and lateral edges of each wall plate; erosion of the top edge is not replaced). The surface was darker and often pitted in these older individuals, probably due to boring algae (Parke and Moore, 1935). These differences in appearance were more reliable than size in separating the youngest age group from all the rest. In fact there was generally some overlap in the size range at this time, as can be seen from Table 4.1. Measurements were made from photographs of the plotted squares which had been under observation for two years. Two year classes had settled in this period and at the time of the photograph were 6 and 18 months of age. Also included in this table are some data kindly provided by Mr. H. T. Powell, from the study of growth rate published in Barnes and Powell (1953); from this data measurements of the same group of animals in their first and second autumns are compared. In three of the four squares of Area 1 and on all of the four panels of Barnes and Powell an overlap in the extremes of size occurred between the

6 and 18 month old groups. There was no difficulty in separating the groups, however, since the largest 6 months old barnacles were the most different from the 18 month group in general appearance. Besides, having smooth thin shells, these fast growing individuals had increased their basal area faster than their opercular opening, resulting in a low barnacle with a proportionally smaller opercular opening. There seemed to be no reliable way to distinguish the various age groups older than 1½ years. Kuznetzov and Matveeva (1949) state that barnacles from the Arctic coast of Russia have definite annual growth rings. Such rings were not obvious at Millport, perhaps because the seasonal variations in climate were not as great as in Russia. No attempt was made to use the method of Parke and Moore (1935); after the second summer the entire shell appeared to be pitted by boring algae.

To indicate the relative amount of exposure to air of the three levels of Area 1 and of the other areas established later, a curve of intertidal height vs. percentage of time submerged was obtained from Mr. H. T. Powell. This curve had provided the information included in Table I of Barnes and Powell, (1953), and was calculated from the Admiralty Tide Table, 1952, corrected for

Millport. The heights above or below MTL, and the percentage submergence for all the areas are given in the Appendix.

Following the settlement seasons of 1953, 1954, and 1955, the newly settled group was counted on each area. On Area 1, where the older barnacles had already been mapped, the new settlers were not mapped individually. Instead, a smaller area surrounded by mapped older individuals was indicated on the map and all the new barnacles in this area counted. To avoid any chance of duplication, each barnacle as it was counted was touched with a small brush containing yellow water colour paint. This washed off in the next few tides. This system was used on the other areas where detailed mapping of every individual was not done. Just before the 1954 settlement season the remaining 1953 individuals were mapped so that the new settlement could then be easily delimited and counted.

In the autumn of 1953, it was decided to set up other census squares at the same three levels on Area 1. Besides providing more replicates as a check on the variability of adjacent areas these new squares more closely resembled the unprotected controls than the caged

squares, whose age structure was quite different from the surrounding population after a year of protection. By December, 1953, there was a total of 16 squares, 6 of them caged, on Area 1. These later squares were larger than the original ones. On all these areas periodic counts were made every 4-6 weeks.

In the summer of 1953, after counts had been made of the new 1953 settlement on the squares of Area 1, two pairs of large boulders were selected to study the survival low in the intertidal zone. It was hoped to keep one of each pair of boulders free of Nucella by hand picking at frequent intervals, but this proved impractical for Boulder 1, so that after a month the attempts at exclusion were stopped. On Boulder 5, which was more isolated, the method was successful in the summer of 1954, but predation by starfish (Asterias rubens) also occurred at this low level. On these boulders in 1953, instead of mapping, a narrow strip was cleared of barnacles around each square and the number inside the boundary simply counted. It was later felt that this was not a good method for delimiting a group of barnacles for periodic counts, since the individuals bordering the cleared strip would be less crowded than those surrounded by other barnacles. Therefore, in the summer of 1954,

pieces of thin glass (cleaned used photographic plates) were placed directly on the rock and the bordering individuals of the square marked directly on the glass with glass-marking ink. Pits drilled outside the area allowed exact orientation of the glass plate for later counts. The glass-marking ink was very tenacious, allowing the plate to be washed without loss of marks. Eventually all the census areas were re-mapped using glass plates, which allowed a much more rapid checking in the field. The maps were traced on to thin paper so that notes could be made at each examination. In the Appendix the total number counted and the area of rock containing this number is given for all the areas studied.

B. The crowding process.

In the latter part of the settlement season the new barnacles on the more densely occupied surfaces were usually touching each other, as shown in the photographs in Figure 4, taken in May, 1954. Further growth, which is quite rapid at this time as has been shown by Hatton (1938), produces certain effects which are commonly described under the general term of "crowding". Some of these effects can be observed directly, as for example the changes in growth form with extreme crowding, or the

displacement described in the present work. Other crowding effects are less obvious, such as the lower average growth rate suggested by Moore (1935) and Chipperfield (1948) and most probably certain unknown results which may tend to decrease the barnacle's resistance to adverse factors.

1. The growth of Balanus balanoides.

Crowding occurs when barnacles are in contact and are actively growing. Deevey (1947) attempted to measure crowding by calculating the number of "binary contacts" per unit area; this number he termed the "crowding coefficient", combining density and size together. But of equal importance in crowding is growth, since with the same number of contacts, more pressure will be exerted between the members of a faster growing population. For Deevey's coefficient to be true, barnacles of the same size (and therefore having the same crowding coefficient at a similar density), must grow at the same rate. Barnes and Powell (1953) have shown that for the first growing season at least, Balanus balanoides individuals at lower tidal levels have greater growth rates in relation to their size than those at higher levels. A knowledge of growth variations between locations and seasons is necessary for a full analysis of crowding.

The growth of Balanus balanoides has been well studied in western Europe. The principal investigators have been Runnstrom (1925) in Norway, Hatton (1938) in Brittany, Moore (1934, 1935, 1936a) in the Isle of Man, and Plymouth, England, Chipperfield (1948) at various places on the east, south, and west coasts of Britain, Corlett (1948) in the Mersey estuary, Sokolova (1951) in Russia, and Barnes and Powell (1953) at Millport, Scotland.

The results of these studies of most relevance to crowding are as follows. Growth is more rapid when there is more water movement, such as on wave-beaten points or in tidal currents, (Hatton, 1938; Moore, 1935; Chipperfield, 1948). These authors all believe that this is the result of more food being brought to the population by the increased circulation.

Moore (1935) noted that barnacles packed closely in a groove grew slower than adjacent isolated individuals. He suggested that the food in the water flowing over the surface is shared among more individuals at a higher density. This suggestion is supported by the observations of Chipperfield (1948), also at Port Erin. Of two similarly situated populations at different densities, barnacles in the less dense group grew to an average length

of 5.8 mm. by October while in the more dense group they reached an average of 4.2 mm. In this experiment the barnacles in both groups were growing without contact. While not conclusive, these observations suggest that there may be local depletion of food in dense aggregations of barnacles. On the other hand, Kuznetzov and Matveeva (1949) suggest that growth is faster at higher densities. Collections were made at three locations in East Murman (Arctic Ocean) at densities of 5, 3 and 2 /cm^2, respectively. Age was determined by growth rings on the wall and opercular plates; the maximum ages were 7 years at the two higher densities and 12 years at the lowest. Whether the larger sizes found at higher densities were the result of the differences in density or location is difficult to decide. Analysis of the proportion of inorganic carbonates to organic matter showed a higher proportion of the latter at higher densities, but the variation was sometimes greater between different locations at the same density. This suggests that other factors besides density may have differed between the areas.

The effect of differences of shore level on growth is discussed by several authors. Moore (1935, 1936a) collected barnacles in the summer; his measurements were

Table 4.2 -- A comparison of the average sizes of *Balanus balanoides* at different intertidal levels in Great Britain and Northern France. Measurements of young and adults were made under various conditions of wave action and sediment content of the water.

Location and Authority	Collecting Station	Environmental Conditions	Shore level at which the largest average size was measured		Relative abundance of *Nucella lapillus* at each location
			Age 2-3 months	Age 14 months	
Plymouth, England. Moore, 1936	Hen Point, Tinside	Much sediment or moderate sediment	Low	Low	Absent or few
	Drake Is. Misery Pt.	Clearer water	Middle	About the same at all levels	Common
Isle of Man Irish Sea Moore, 1935	Bradda Head	Heavy wave action	Low	Low	Few
	Dub Reef Alfred Pier Port St. Mary	Moderate to no waves	Low	High	Common
St. Malo No. France Hatton, 1938	Decollé Ouest	Heavy Waves	Low	Low	Probably few
	Decollé Est	Sheltered	Low	High	Probably common
	Cité	Sheltered, strong current	Low	High	Probably common
Millport, Scotland Barnes & Powell 1953	Panels on Keppel Pier	Sheltered, strong current	Low	Low	None

separated into the 2-3 month old group and the 14 month and older groups. Hatton (1938) and Barnes and Powell (1953) followed the growth of individuals, mapped on the shore or on panels attached to a pier. To compare the sizes at different shore levels at the different locations, the average sizes at age 2.5 months and at 14 months were taken from the growth curves given in the last two papers. The level at which the largest average size occurred in all these studies is given in table 4.2.

Except at two locations near Plymouth, the largest barnacles at 2-3 months after attachment were found at the lowest levels. After a year, however, some locations showed a reversal of this situation while others did not. Moore considered that this apparently slower growth at low levels might be due to a harmful factor in the water which retarded the growth of older barnacles; this would act most strongly at low levels. With greater wave action or a higher content of suspended matter in the water, he suggested that increased food supply might outweigh the harmful effect of immersion. There is no evidence to support this suggestion; it seems unlikely that the growth of a marine species would be harmed by immersion in the sea. Sokolova (1951) found that Balanus

balanoides in Russia grew faster the longer they were immersed.

Barnes and Powell (1953) suggested that the greater sizes which Moore and Hatton found at high levels may have resulted from the high level barnacles growing faster in the second season because of their smaller size at the start of the season. However at the end of the second season the largest average size of Barnes and Powell's barnacles was still at the lowest level, despite the slightly greater relative growth rate which they found at high levels in the second season. Therefore, it is unlikely that the larger sizes at higher levels found in the other studies could have resulted from such growth rates.

Certain data collected in the present study suggest another cause for these differences. If mortality occurs more heavily among the larger or smaller sizes, the average size will become different from that of a group where the mortality is random with regard to size. In section VI of this study it is shown that Nucella lapillus selected larger barnacles as prey. Furthermore, Nucella is more abundant at lower shore levels. Therefore, where Nucella is an important predator, the barnacle population, after a sufficient interval of time,

will contain a disproportionate number of the smaller individuals. As Barnes and Powell (1953) have shown, the differences in average size between levels at 14 months is not great, so that a moderate amount of selective predation by Nucella at lower levels might be enough, to reduce the average size below that of the highest level, where Nucella is infrequent. That selection against larger sizes does occur is shown in the growth curves of Hatton (1938). Decreases in average size of 0.7 mm occurred at the lowest levels in the first autumn. These decreases were explained as due to erosion by Hatton and Fischer-Piette (1932), but in his 1938 paper, (page 268) Hatton suggests that the irregular outlines of the barnacles may have caused the decreases in mean size. That this amount of erosion should take place seems unlikely, and errors of measurement due to irregularity would be likely to compensate each other, especially since the same individuals were measured each time. As Deevey (1947) suggests, there was probably a relatively greater mortality of the larger individuals.

In table 4.2 the relative abundance of Nucella between stations at various locations is given. Moore (1935) observed that Nucella was absent or uncommon where heavy sediment or great wave action occurred. From this

it was deduced therefore, that Decolle Ouest in Hatton's study would have had the least predation by Nucella of any of his three areas. The stations where Nucella was absent or uncommon were also those where the average size of adult barnacles remained greatest at low shore levels. At the stations where Nucella was more common, the greatest average size was found at high levels. This correlation appears to uphold the hypothesis that the smaller average size found at low levels was the result of greater mortality of larger individuals at this level.

Seasonal variation in growth is very marked, most occurring in the late spring with some evidence of another growing period in the autumn (Runnstrom, 1925; Chipperfield, 1948). The second year's spring growth brings the barnacle almost to its maximum size, with some further slight growth in the following years.

From these growth data, it would be expected that crowding would be most intense during the first six months of life, followed by a slackening during the first winter and a renewal of crowding during the second spring and summer. During the first growing season, crowding at similar densities would be expected to be more intense lower on the shore. The effects of these variations in crowding on mortality will be discussed in a later portion of this section.

2. Results of extreme crowding.

Descriptions of the modifications in growth form of Balanus balanoides caused by rapid growth of crowded populations are given by Trusheim (1932), Hatton (1938), Schafer (1948), Barnes and Powell (1950), and Sokolova (1951). These papers describe how individuals with no room to grow except vertically, elongate into local "buissons" or hummocks, which are poorly attached to the rock, the extreme individuals being trumpet-shaped. Sokolova (1951) gives the ratio of length of base to length of aperture for populations of Balanus balanoides at different densities. In their second summer, populations with a density of about $4/cm^2$ had individuals of a columnar form, while those with densities above $7/cm^2$ were trumpet-shaped.

In the summers of 1953, 1954, and 1955, such extreme "hummocking" was observed on the study area, usually near the lower limit of Balanus balanoides distribution. Even above MTL, instances of individual hummocks coming away from the rock were noted in these years.

During the growth into hummocks high mortality occurs. Barnes and Powell (1950), dealing with mixtures of Balanus crenatus and Balanus balanoides on panels hung from a raft at Millport, counted $36/cm^2$ of

new set in April. Eight weeks later hummocks were well developed, and a density of about 5/cm^2 was noted in a hummock, though very few large dead individuals were present. Thus, about 86% mortality due to hummock formation occurred in only 8 weeks.

In 1954, deaths caused by hummock formation on the intertidal rock were determined. In one area at about MTL, counts of newly settled individuals were made on six occasions from May 8 - 25th. On October 11th, three hummocks were carefully collected from the same spot, and the area of attachment which was left bare after collection was measured with a centimetre grid. This was also done on two other areas where the density had been counted June 4th. The percentage death in the first three hummocks was 52, 34, and 59. For the other two areas it was 34 and 57. The highest individuals in the first four hummocks were 1.2 or 1.3 cm., while the last, located on a very wave beaten reef, had extreme individuals of 2.1 centimetres height. The highest individuals measured in intertidal conditions by Barnes and Powell were similar to the first measurements, 1.3 cm.

In these intertidal hummocks there were usually some shorter individuals attached near the top of the elongated individuals. In the hummock with extremely

long individuals noted before, 32 of the 84 individuals were so attached. When this area was first examined in June 4th, all the new barnacles were attached to the rock surface with a density of 44/cm.^{2}; settlement had entirely ceased on the cleared areas on the stones, nearby. It appears certain, therefore, that the short individuals had been undercut and lifted, becoming attached to the longer ones in the process. This process has been witnessed in several individual cases on the plotted areas of the stones, particularly on Stone 3 where the initial density remained high during the first period of rapid growth. According to Dr. H. Barnes, (personal communication), this undercutting with growth is often witnessed in anti-fouling panels, where even pencil marks on ground glass adjacent to barnacles were lifted on to the side of the barnacle. This conclusion is at variance with that of Barnes and Powell (1950), who believed that the smaller individuals attached to the elongated ones on the shore were derived from a later settlement.

To test whether such hummock formation, denoting extreme crowding, results in greater mortality than crowding without hummocks, the following counts were made. On panels hung intertidally below Keppel Pier,

Table 4.3 -- The percentage mortality of Balanus balanoides during the six months after settlement on a panel suspended at MTL from Keppel Pier, Millport, June to October, 1954. Several small areas which exhibited the "hummock" growth form and adjacent areas with similar densities where "hummocks" did not form are compared.

Portion of Panel:	Top	Middle	Bottom
Percentage death in a hummock :	18 43	37 40 40	67
Percentage death when no hummock formed	39	2 14	33

counts of settlement were made on June 1st. On October 11th, the panels were brought in and counts were made both of hummocks and of adjacent areas. On these intertidal panels, the distributions in June appeared to be quite even; the percentage mortality was calculated from the difference between the June and October counts. Four panels were examined but only the uppermost will be mentioned here, since it alone bore a pure population of Balanus balanoides. The densities of June 1st at the top, middle and bottom of the panel were 19.9, 20.8 and 20.9/cm.^{2} respectively. Table 4.3 gives the percentage mortality in the two situations.

In general the faster growth leading to hummock formation appears to cause greater mortality.

Thus extreme crowding, while resulting in great modification of growth form in the survivors, also causes crushing and displacement of the others which die in the process. In wave beaten situations, the final result is total loss of the hummocks as described by the previously mentioned authors. This also happened in the autumn of 1953, 1954, and 1955 on the present study area, as will be described later.

3. Results of less extreme crowding.

In the instances where hummocks formed, mortality continued into the winter when growth had ceased. Where crowding occurred due to high density at the upper shore levels, hummocks were not usually formed. But some modifications of growth form occurred nevertheless. The earlier settled or larger barnacles generally assumed the cone shape of an uncrowded barnacle. The medium sized individuals, especially those which attached during the short period of very intense settlement, often became columnar in shape. The smaller or slower growing individuals were undercut and lifted, or were forced into trumpet-like shapes. These later forms were much less firmly attached than the normal cone-shaped barnacles. As a result, the mortality during the winter, when growth slowed down,was higher in populations where the density at the end of settlement was high. This can be seen in Figures 16 and 17, which compare the mortalities of different densities of the 1954 settlement in the caged populations. Where the initial densities were low, the curves flatten out in winter, indicating a lower relative mortality rate; at high densities the mortality rate remains high through the winter.

C. The results of the studies of crowding.

1. Areas above MTL.

To compare the effect of crowding on survival on Area 1 and stones 1-8, the average length of life was calculated for a span of 180 days, beginning a month after settlement had ended. Since the settlement occurred about a month later in 1954 than in 1953, the starting dates were June 1 in 1953 and July 5, in 1954. Except for stones 1 and 2, all the areas were above MTL. The results of these calculations are given in Figure 8. With increasing density, the average length of life generally decreased for the span considered.

Certain exceptions to this general trend were evident. On Area 1, in 1953, the greater densities at the Upper level did not result in a marked shortening of the length of life. A comparison of the separate levels of Area 1 in 1954 shows that the points of the Upper level lie to the left at any particular length of life. This pattern seems to indicate that the populations at higher shore levels could survive better at higher densities than could those at the lower levels. The studies cited previously have shown that relative growth rate decreases with increasing height on the shore.

Figure 8. The effect of density at about a month after settlement, on survival during the next six months. The periods used were June 1 to Nov. 28, 1953 and July 5 to Dec. 31, 1954.

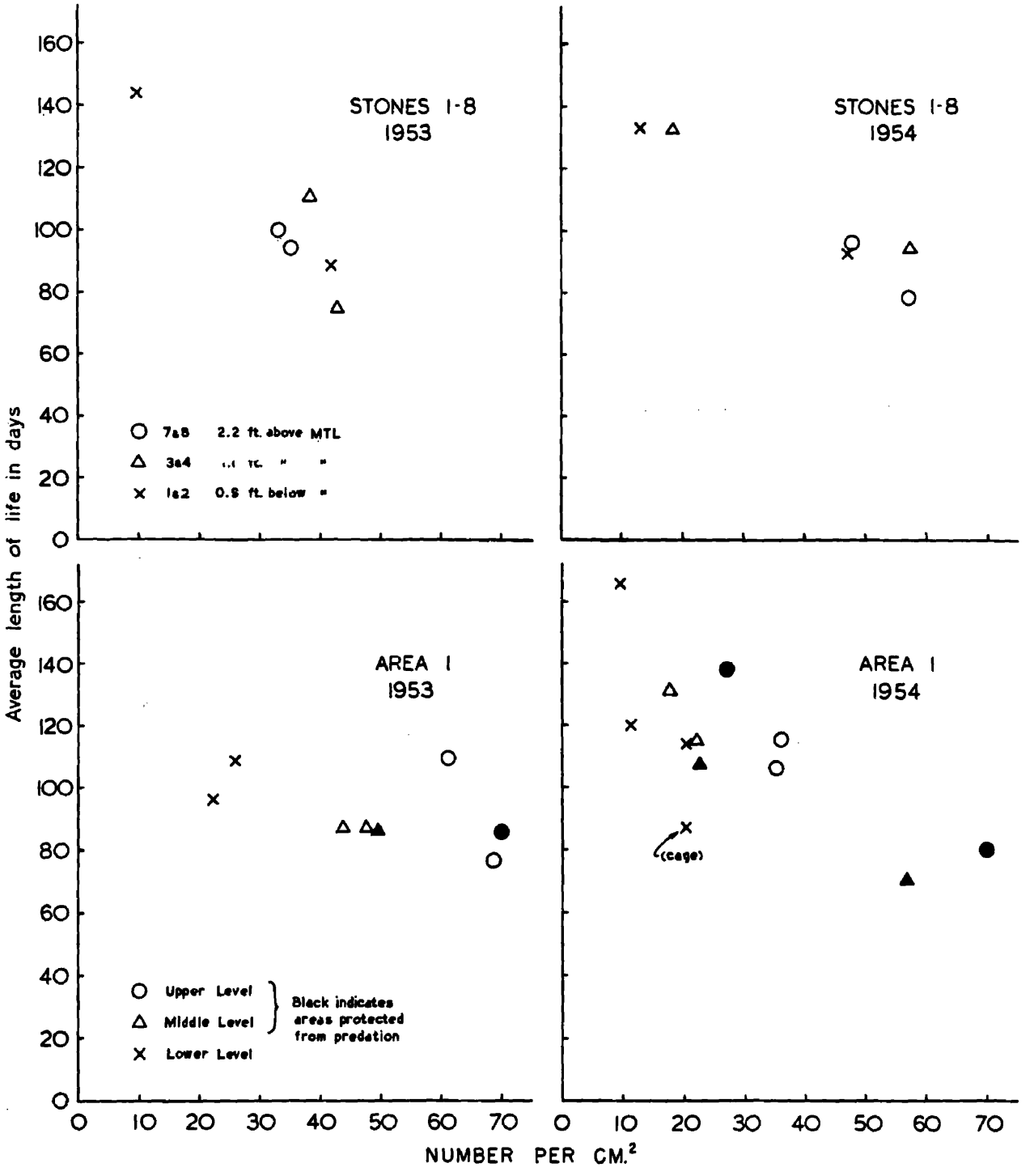
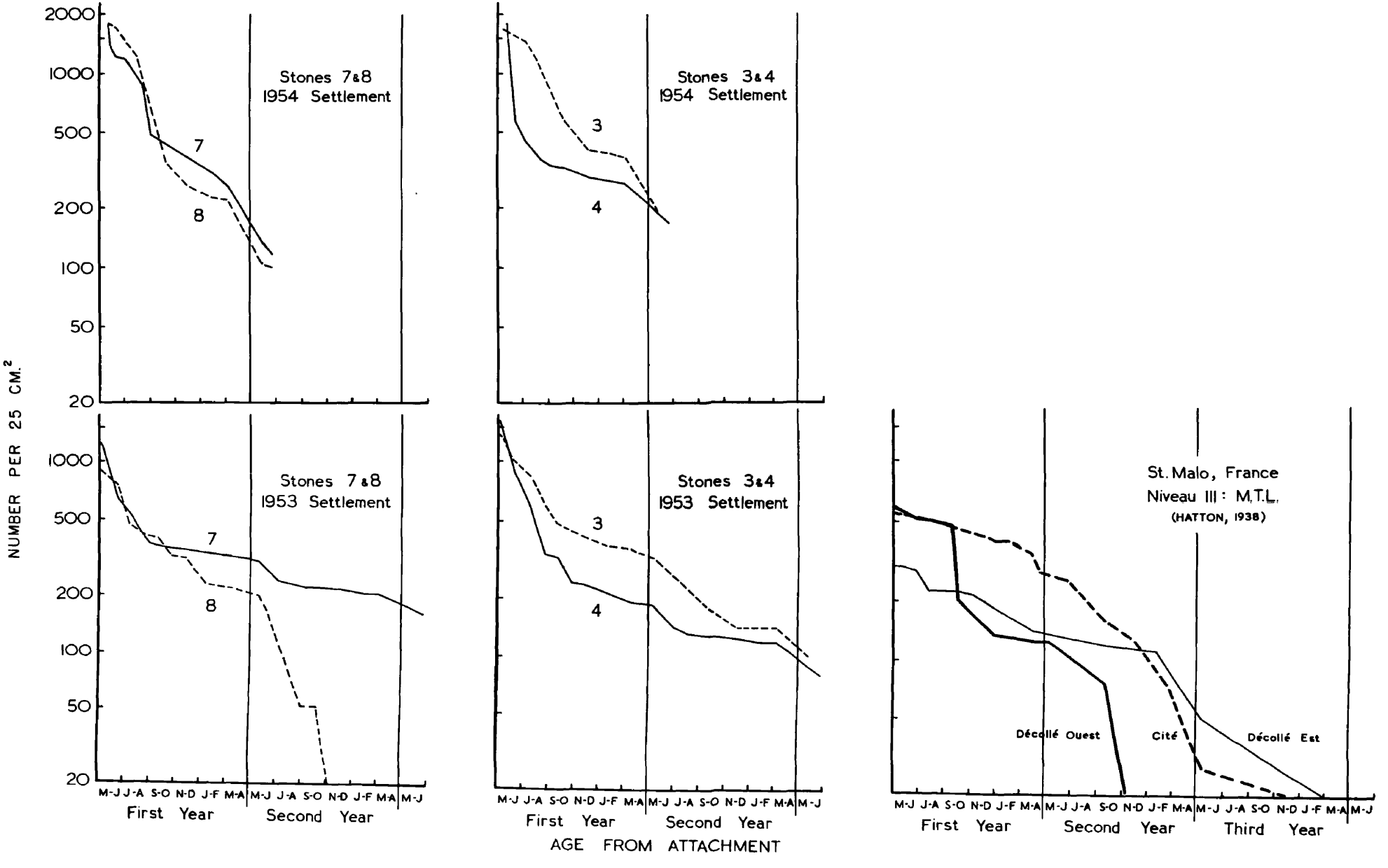

STONES 1-8
1953
STONES 1-8
1954
AREA 1
1953
AREA 1
1954
Average length of life in days
NUMBER PER CM.²
7&8 2.2 ft. above MTL
3&4 1.1 ft. " "
1&2 0.8 ft. below "
Upper Level
Middle Level
Lower Level
Black indicates areas protected from predation
(cage)
0
10
20
30
40
50
60
70
80
100
120
140
160

Figure 9. The survival of Balanus balanoides at various locations just above MTL at Millport and on the shore in Brittany at about MTL in 1930-1933.


NUMBER PER 25 CM.²
2000
1000
500
200
100
50
20
Stones 7&8
1954 Settlement
7
8
Stones 3&4
1954 Settlement
3
4
1000
500
200
100
50
20
Stones 7&8
1953 Settlement
7
8
Stones 3&4
1953 Settlement
3
4
St. Malo, France
Niveau III : M.T.L.
(HATTON, 1938)
Décollé Ouest
Cité
Décollé Est
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
Third Year
AGE FROM ATTACHMENT

The slower growth acts to alleviate the effect of high density on survival at the upper shore levels.

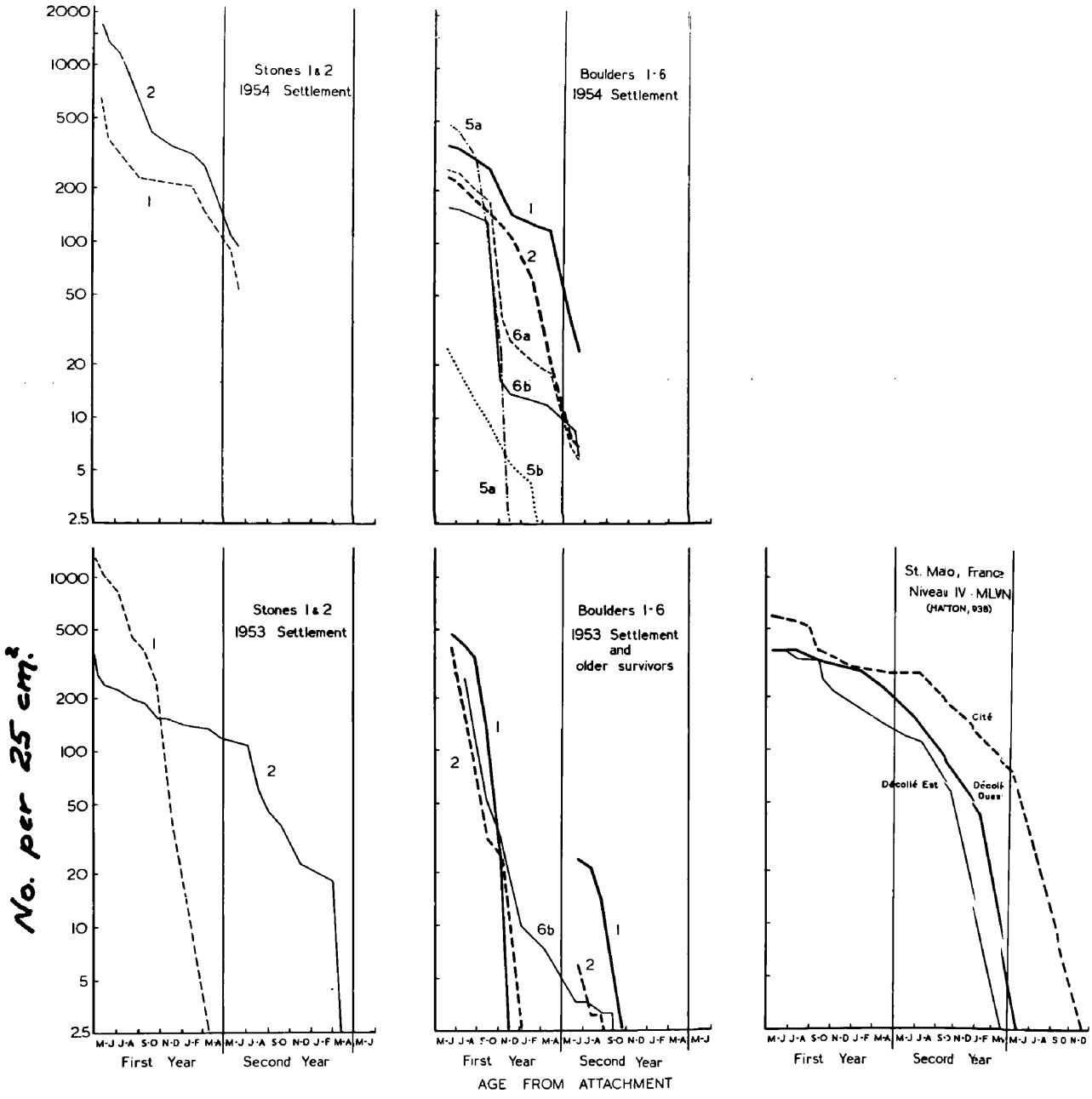
A marked seasonal variation in relative mortality rate is evident from the survival curves shown in Figures 9 and 10. The relative death rate decreases in winter as shown by the flattening of the curves.

2. Areas near the lower intertidal distribution of Balanus balanoides.

The survival curves for barnacles near the lower limit of their intertidal distribution are shown in Figure 10. Predation was intense at this level and all attempts at elimination by picking off the whelks were only partially successful.

In 1953, the initial densities on boulders 1 and 2 were 20/cm.^{2} and 18/cm.^{2} respectively. For the first month of observation the whelks were picked off boulder 1. This control was then abandoned but the absence of predation had allowed the density to remain high and fast growth had resulted in extreme crowding into hummocks, as described earlier. The hummocks began to break off in August, and by December, all the barnacles had been washed off this boulder. There was little hummocking on boulder 2, probably because the heavy

Figure 10. The survival of Balanus balanoides below MTL, just above the lower limit of its intertidal distribution. The St. Malo data are from a slightly lower level.


Stones 1 & 2
1954 Settlement
Boulders 1-6
1954 Settlement
Stones 1 & 2
1953 Settlement
Boulders 1-6
1953 Settlement
and
older survivors
St. Malo, France
Niveau IV - MLVN
(HATTON, 938)
Cité
Décollé Est
Décollé Ouest
No. per 25 cm²
2000
1000
500
200
100
50
20
10
5
2.5
1
2
5a
5b
6a
6b
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
AGE FROM ATTACHMENT

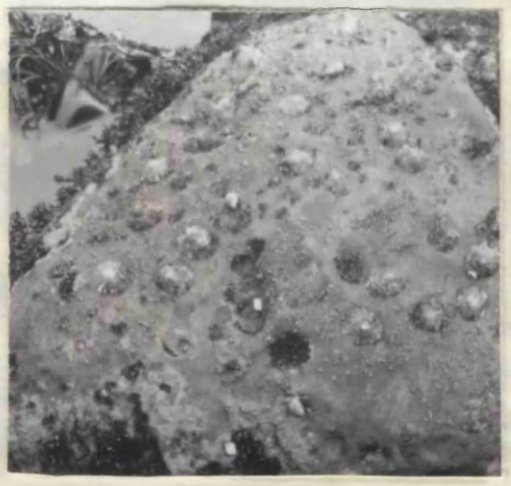
predation by Nucella had thinned out the population so that during their period of fast growth the individuals impinged on each other less. The photographs of Figure 11 illustrate these changes.

In 1954, the only boulder with a high density was boulder 5a; the Nucella were kept off this boulder most of the summer and hummocks formed as before, resulting in elimination of the population by November. On the other boulders the initial density was low, no hummocks developed and survival was good. With the slowing of growth in winter the death rate dropped, rising again the next spring when growth began again. As is shown in section VI, the degree of predation during the summer and autumn of both years was approximately the same on boulder 2, so that the reason for the poorer survival in the first year was probably related to the initially higher density. The reason for the better survival at low levels shown in Hatton's curves is not known. If the growth rates were slower than at the same level at Millport, there should be less crowding at St. Malo at the same densities.

To obtain an estimate of the growth on the shore at Millport for comparison with Hatton's data, photographs of the same area at MTL, taken in June and November, 1954,

Figure 11. The complete destruction of the 1953 year class low on the shore, resulting from the development of unstable growth forms under conditions of intense crowsing. There was less crowding on Boulder 2, but heavy predation eliminated the survivors. (Scale x 1/10)


August 9, 1953

November 14, 1953


March 26, 1954

Boulder 1.

Boulder 2.

Table 4.4 -- Comparison of the growth rate of Balanus balanoides at Millport and St. Malo. All barnacles were growing without contact on intertidal rocks.

Millport, just above and below MTL.

June 11, 1954		Nov. 3, 1954		Mean specific growth rate per day
Number measured	Ave. length in mm.	Number measured	Ave. length in mm.	
39	1.9	27	4.8	0.59

St. Malo, data from Hatton (1938). Level III, just below MTL. About 50 individuals in each measurement.

Location	Date when average length was 1.9 mm	Greatest average size reached in the first six mos.		Mean specific growth rate per day
		Date	Length	
Decolle Ouest	April 15	Aug. 25	3.4	0.44
Decolle Est	May 10	Aug 25	3.0	0.42
Cite	April 18	Aug 20	3.5	0.48

Note: The mean specific growth rate is the increase in length per unit length per day X 100.

were used. Isolated individuals of the 1954 settlement were measured in the two sets of photographs; a scale was included in the photographs. To obtain the growth rate from Hatton's data, the sizes late in August, 1930, were taken from his curves of level III, MTL. This was the date when the maximum size was reached at St. Malo; after this the curves decreased, probably because of selective predation. All the growth rates were calculated as beginning at the same average size as that found at Millport, 1.9 mm. The time interval from Hatton's curves was taken between the date when the average size was 1.9 mm. and the date of maximum size in late August. These readings and the calculated mean specific growth rates are given in Table 4.4.

This method, using only the period of apparent maximum growth at St. Malo, while taking a longer span for the Millport measurements, probably tends to underestimate the Millport rates as compared to St. Malo. However, the growth rate is still greater at Millport. At the same density and shore level, crowding would be expected to be more intense at Millport.

In the spring of 1953 and 1955, survivors of the previous year's settlements were present on these low

shore areas. In the spring of 1954, there were no survivors on the boulders where dense settlement had occurred the previous year. The settlements of these three spring seasons varied, being high in 1953 and 1955, low in 1954. In the discussion of settlement it was suggested that this situation might occur if the presence of adults stimulated settlement. Since survival seems to vary inversely with the density of settlement, good survival following a light settlement would stimulate a heavy settlement the next year. This would be followed by poor survival due to hummock formation. The absence of survivors the next spring would thus result in a light settlement. This cyclic sequence is over-simplified, since intense predation might cause very poor survival even in years of light settlement, and other natural disturbances could occur.

The settlement density of 1952 is not known but some barnacles survived until June 1953. Some members of 1954 settlement likewise survived over a year. The 1953 and 1955 settlements suffered destruction during the winter. This suggests an internally regulated cycle, similar to that demonstrated in the laboratory with blowflies by Nicholson (1954). With a constant supply of food the population underwent fluctuations, since at low

densities there was plenty of food and many eggs were laid, while at high densities there was not enough food to allow reproduction. In the present case, when mortality from crowding was low following a light settlement, the adults which survived during the next spring season apparently attracted a heavy settlement. These grew into unstable hummocks and were all lost; the bare boulders the next spring received only a light settlement due to the absence of adults. A much longer set of observations would be needed to show whether such a cycle would continue. The factors necessary for it: sufficient larvae each year, the gregarious behaviour of settling larvae and the inverse correlation of initial density and survival, have all occurred in the three years of this study.

3. Mortality due to crowding after the age of six months.

In examining the mortality of older barnacles for evidence of crowding, only those areas which were protected from predation were used; this limits the analysis to the caged populations on Area 1. From Figures 16-18 it can be seen that the rate of mortality of the barnacles inside the cages became progressively lower with increasing

age. There was some seasonal variation, mortality usually decreasing in winter and increasing in the spring. However, there was enough variability between areas to conclude that the decrease in growth after the age of 18 months was not followed by a complete cessation of crowding. In addition, it is probable that members of a younger fast-growing group had some effect on the older individuals with which they mingled. To investigate these possibilities, a more detailed study of the mechanisms of crowding was made.

D. The causes of mortality due to crowding.

To analyze the causes of death in crowded situations, photographs taken at intervals of some of the counted areas were examined. For the crowding during the first growing season, photomicrographs of portions of the plotted areas of Stones 7 and 8 were taken at about ten day intervals in the late spring of 1955. For the older groups, photographs taken on the shore in February of 1953, 1954, and 1955 of the Middle Cage 1 square were used. Stones 7 and 8 and the Middle Cage were all within one metre distance at exactly the same level on Area 1.

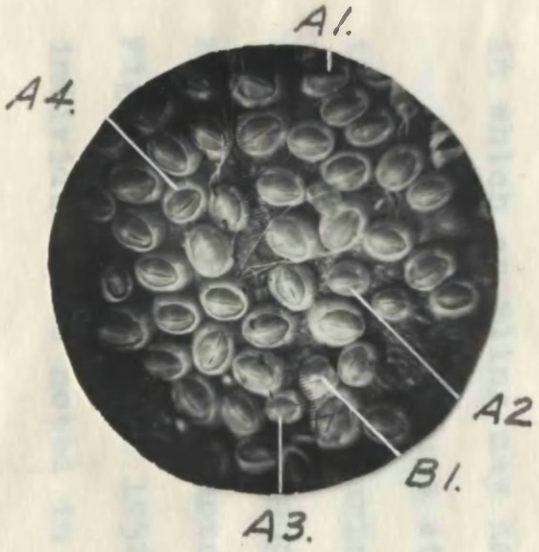
Figure 12 shows the series of photographs of Stones 7. Certain individual barnacles are marked so that their

Figure 12. Photomicrographs taken at intervals following settlement of one area on Stone 7 in 1955. (x5.2) Some examples of the effects of crowding are shown. The individuals are marked as follows:

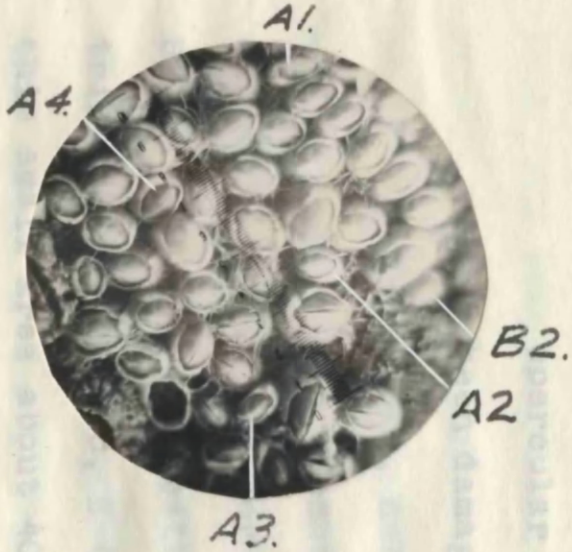
A. Barnacles being crushed laterally.

B. Barnacles being undercut and displaced.

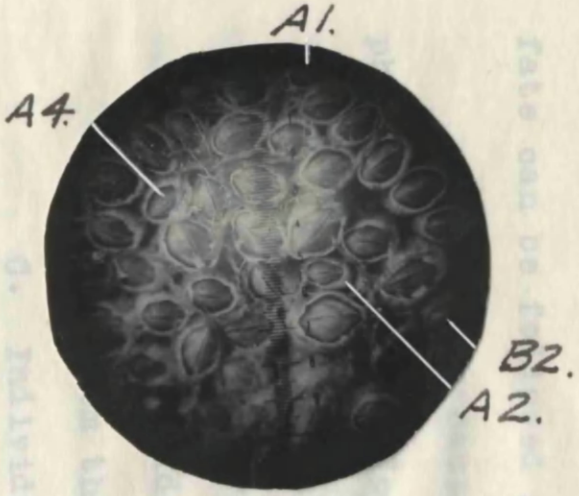
C. Barnacles whose shells have been broken, probably by water-borne objects.



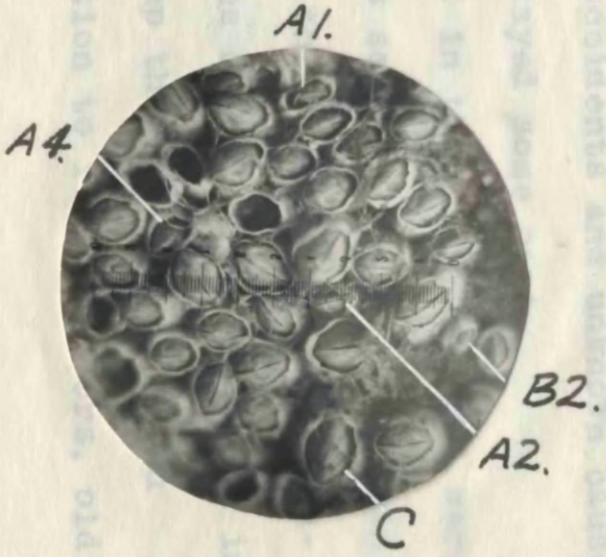
April 29



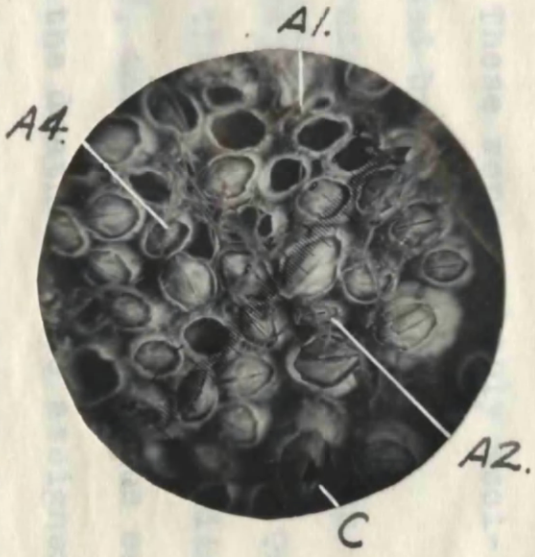
May 11



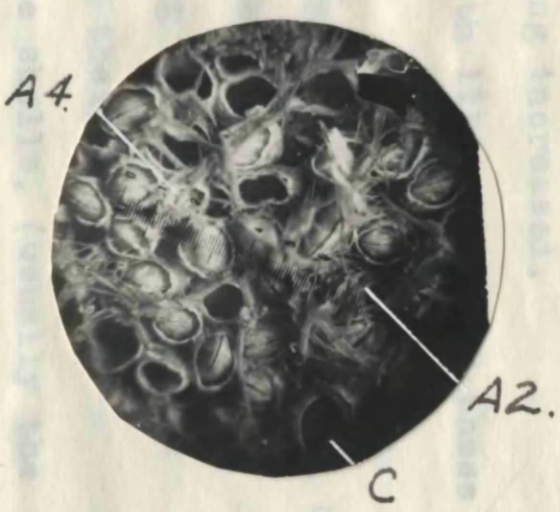
May 21



May 30



June 10



June 19

fate can be followed as crowding increased.

The three causes of death illustrated by these photographs are as follows:

A. Individuals being laterally compressed by pressure from their neighbors.

B. Individuals being undercut and tilted from the rock by their neighbors.

C. Individuals whose shells, (usually the opercular valves in these cases) have been damaged. These were probably accidents, not caused by crowding.

The unmarked empty barnacles died from unknown causes, and account for the majority of the deaths. On Stone 7, of the 24 deaths in the 52 day period, the distribution was: A-6, B-4, C-2, and unknown-12. Thus on this small area about 40% of the deaths can be assigned to crowding and the rest to accidents and unknown causes, in which crowding may have played some part.

The age groups studied in the Middle Cage 1 were the 1952 age group during its second growing season in 1953 and the older groups in their third or later seasons. A series of photographs of this area is shown in Figure 19. For the 1952 group the position of each individual was noted in relation to its neighbors, old

and young, and its fate noted a year later. Of the 62 individuals in the 1952 group, 48 died in this second growing season; from the analysis of the photographs, 31 of these deaths were tentatively ascribed to crowding. Small barnacles were sometimes overhung by others of the same age which had attached to the sides of large older individuals. These upper epizooic barnacles seemed to grow more quickly and may have prevented some of the food from reaching the ones below them, or by their growth they may have crushed the lower ones. Certain of the small barnacles which died were located between medium-sized older barnacles which had grown in the interval between photographs and may have crushed the smaller ones. Of the seventeen other deaths, nine were of individuals attached to dead adult shells which fell off, carrying the living younger ones with them. In the survival curves of Figures 16-18, the younger barnacles attached to other adult barnacles were not included, so that this cause of death is excluded.

In this same analysis some reasons for the deaths of the older barnacles can be deduced. Of the twenty-one barnacles of the pre-1952 group which died in the Middle Cage 1 during the first two years study, four were smothered by younger barnacles which attached near their

opercular openings and grew partly over them.

Five were of small size and were probably crushed by the surrounding individuals which all grew slightly; two were partly attached to a larger dead adult which fell off, carrying the others with it; ten died without apparently being crowded or smothered. Some of these last ten were very large and may have died of old age, probably a rare occurrence in natural populations in general. However, in the level near the top of the distribution of Balanus balanoides, where predation is probably almost totally absent, very large weathered empty shells were fairly common. In this situation, deaths from old age may be a regular occurrence; the protection given by the cages on area 1 seems to have duplicated this situation at a lower level.

As was expected from the variations in growth, crowding is intense in the first and to a lesser degree in the second spring growing seasons, and its effect on growth form may cause delayed mortality during the first winter. After the age of 18 months, in the absence of predation, about half the deaths may be caused by crowding, either by further growth of the same age group, or smothering by younger ones; the remainder die from unknown causes, some perhaps from old age.

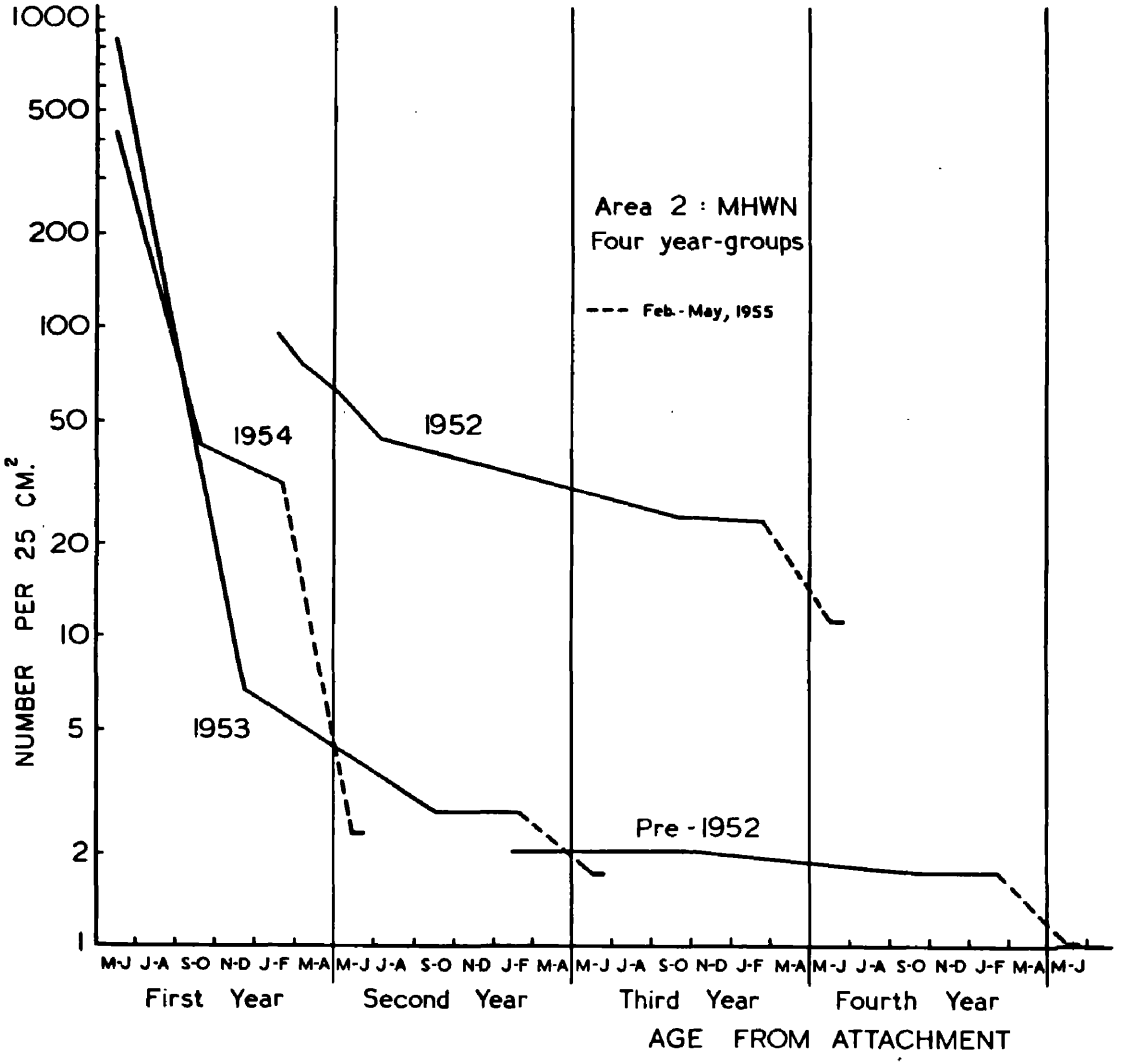
V. Mortality at high shore levels.

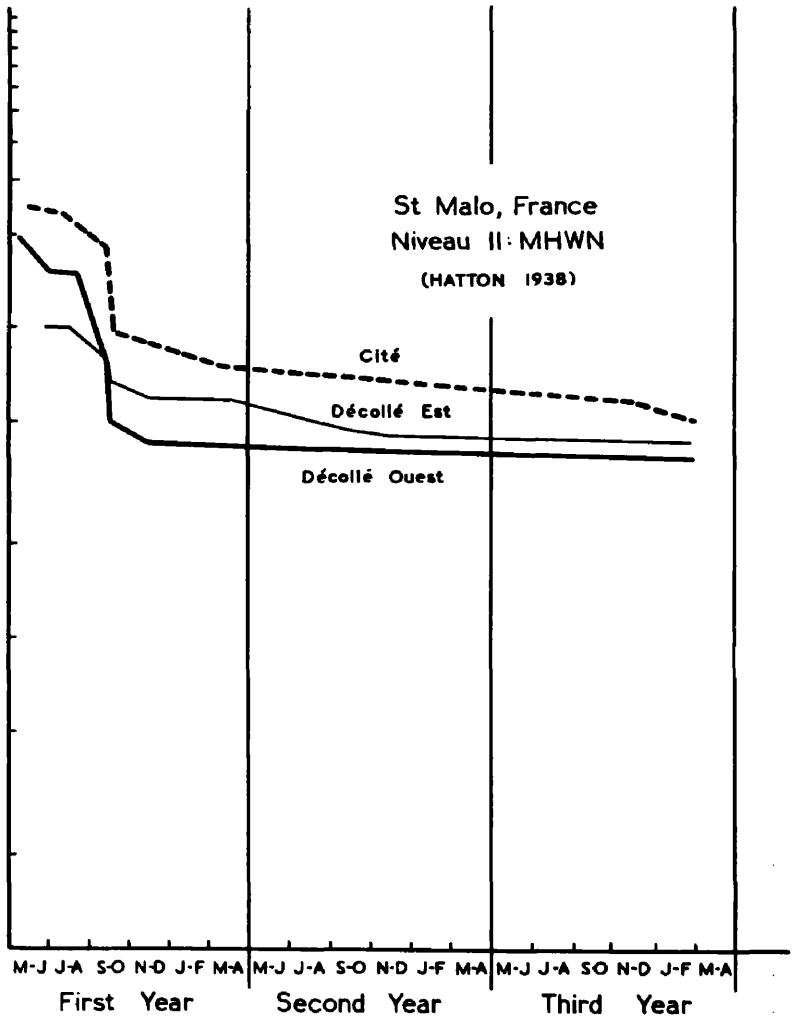
1. The upper limit of Balanus balanoides distribution.

Near HWN the upper limit of distribution of Balanus merged into the bottom of the narrow Chthamalus stellatus zone. Little crowding occured here since density was low and growth slow. Three squares were mapped above MHWN on the rock face above Area 1. A cage and netting "cover" were attached at first, but since no Nucella were ever observed at this level and since the survival was the same after a year on all squares, the cage and cover were removed. The results of these counts are given in Figure 13, all three squares being combined. This will be referred to as Area 2.

In the first mapping in December, 1952, the 1952 year class was distinguished from the previous settlements by its smaller size and the smoother appearance of the shell surface. As explained earlier this method is probably valid for distinguishing the youngest age class from older classes. Because of the slow growth at this level the average size difference between the first and second year individuals was less than that of the populations low on the shore. For the small

Figure 13. The survival of Balanus balanoides on Area 2, near MHWN where it was mixed with Chthamalus stellatus; survival curves at the same level in Brittany in 1930-1933 are also shown.


1000
500
200
100
50
20
10
5
2
1
NUMBER PER 25 CM.²
Area 2 : MHWN
Four year-groups
--- Feb.-May, 1955
1954
1952
1953
Pre - 1952
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
Third Year
Fourth Year
AGE FROM ATTACHMENT


St Malo, France
Niveau II : MHWN
(HATTON 1938)
Cité
Décollé Est
Décollé Ouest
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A SO N-D J-F M-A
First Year
Second Year
Third Year

group of individuals where uncertainty existed, the numbers were divided equally between the 1952 and the older group.

Stones 5 and 6 were attached at the same level about thirty feet away, one under an overhang, the other facing up. Since the settlement and mortality were very similar on both stones the results have been combined.

The data from Area 2 and from the equivalent level at St. Malo from Hatton's (1938) study are shown in Figure 13. At both places the greatest mortality occurred in the first six months after attachment. The survival was good after this except for the spring of 1955 at Millport; this heavy mortality will be discussed later.

The curves in Figure 13 are arranged so that the survival of the different year classes can be compared at the same age. Only the 1952 year class survived well after the first year of life, and except for a short time after each settlement season, outnumbered the other year classes for the whole study period. Variations either in initial settlement or in mortality after settlement could accout for this. In Table 5.1 the densities at settlement and in the first autumn after settlement are analyzed for variability between years on all the areas studied.

Table 5.1 - Annual variations in the densities of Balanus balanoides at settlement at Millport and St. Malo (Hatton 1938), and at age 6-8 months at Millport

	Feet from MTL	No./cm.^{2} at end of set					No./cm.^{2} at age 6-8 months				
		1953	1954	1955	Ave.	% Ave. deviation	1952	1953	1954	Ave.	% Ave. deviation
Area 2	+4.2	34	17	18	23	32	2.8	0.3	1.7	1.6	54
Stones 5 & 6	+2.5	16	14	18	16	12	---	0.0	---	---	--
Area 1, Upper	+2.6	67	42	56	55	16	5.6	5.2	16.0	9.0	52
" , Middle	+2.1	47	31	48	42	17	6.7	5.3	12.5	8.1	36
Stones 7 & 8	+2.2	34	52	35	40	19	---	13.6	16.0	14.8	8
Area 1, Lower	+1.5	24	15	42	27	37	6.7	6.2	8.7	7.2	14
Stones 3 & 4	+1.1	40	38	57	45	18	---	13.7	17.8	15.7	13
Stones 1 & 2	-0.9	34	52	30	39	23	---	7.9	13.0	10.4	25
Boulders 1,2,6	-1.3	17	10	25	17	29	---	1.1	4.4	2.7	59

No. per cm.^{2} at end of settlement near St. Malo, from Hatton (1938)

Level	Decolle Ouest				% ave. deviation	Decolle Est				% ave. deviation	Cite				%ave. deviation
	1930	1931	1932	Ave.		1930	1931	1932	Ave.		1930	1931	1932	Ave.	
II(HWN)	8.0	5.8	---	6.9	16	4.0	5.2	---	4.6	13	10.0	11.4	---	10.7	7
Between II&III	23.0	20.0	19.5	20.8	5	12.0	12.5	13.0	12.5	3	22.0	19.5	18.5	20.0	7
III(MTL)	23.2	20.2	---	21.7	7	12.1	12.9	---	12.5	3	22.1	19.9	--	21.0	5
IV(LWN)	15.3	17.5	--	16.4	7	15.0	13.1	---	14.0	7	23.8	13.9	---	18.9	26

At the extreme high and low levels the variability between years was greater at the age of six months than at settlement. At mid-tide levels the variability at settlement was similar to that at the other levels but the densities after six months were much less variable between years. Thus the phenomenon of a "dominant year class" seems to occur only at the extremes of the intertidal distribution and seems to be caused by variations in mortality rather than in density of settlement. On Area 2 the almost complete destruction of the 1953 class soon after settlement eliminated that group; for the 1954 class the early mortality was lower but the mortality at eleven months of age greatly reduced the density. The 1952 group probably had an unusually favorable period in early life and was able to better withstand the heavy mortality in 1955, apparently by virtue of its greater age.

Annual variation in the numbers of marine animals has often been observed. The importance of dominant year classes in commercial fish was recognized by Johan Hjort in 1914. In his review of 1926 he ascribes the causes either to failure of the larvae to find food immediately after hatching or to the drifting of the larvae away from the proper nursery areas. Sette (1943) made an ex-

tremely careful study of the early mortality of mackerel off the east coast of America. He concluded that drift of older larvae away from proper grounds was the reason for the failure of the year class which he studied.

Walford (1938), Carruthers et al (1937, 1938, 1951), and Chase (1953) all came to the same conclusion for haddock populations. Parrish (1949) concluded that neither the numbers of eggs spawned nor the mortality after the haddocks became bottom dwellers could account for the failure of certain year classes; the pelagic phase was the critical one. In the Balanus populations studied it appears that there were always enough larvae to populate the shore but that high mortalities up to a year after settlement could account for the failure of a year class. The absence of dominant year classes at mid shore levels is due to the occurrence of lower mortality. The planktonic phase in the life of a barnacle seems to be less critical than that of fishes. Thorson (1950) maintains that the mortality in the pelagic larvae determines the numbers of bottom invertebrates in Denmark but gives no evidence of variation in settlement and later mortality so that this hypothesis remains unproved.

Table 5.2 -- Mortality of Balanus and Chthamalus from Feb. 13, to May 28, 1955 on Area 2, HWN.

		Age group			
		Older than 1952	1952	1953	1954
Number present, Feb.: (on 75 cm.^{2})	Balanus	5	70	8	93
	Chthamalus	173	42	143	159
% Mortality by May:	Balanus	40	53	37	92
	Chthamalus	0	0	5	62

2. An unusual occurence of high mortality in the upper shore levels.

In April and May, 1955, a high mortality occurred at and above the upper level of Area 1, as shown in Figures 13 and 16. This mortality might have been expected among the barnacles which were still growing and crowding each other but its occurrence among older barnacles inside the cages at the upper level and on Area 2 was very unusual. This high mortality rate did not continue during the following examination period in late May and June.

Predation was not involved since the caged populations also suffered this mortality; no instances were observed of older barnacles being smothered by younger ones. The mortality of the Chthamalus on Area 2 is compared to that of Balanus in Table 5.2. All ages of Balanus suffered heavy mortality, while only the youngest Chthamalus died. A similar but lesser mortality occurred at the Middle level but almost none at the Lower level of Area 1. Possibly the heavy mortality was related to some deleterious effect of exposure to air.

A tide gauge had been operating for a year previously at Keppel Pier, 1/2 mile north of the study area.

Table 5.3 Dates from April, 1954 to May, 1955, when the High Water did not rise above 8.5 feet, O.D., the height of the Upper level, Area 1.

Number of successive high tides 8.5' or less		Dates of occurrence.
One	1954:	Apr. 12, 26, 27, 28 July 12 Sept. 22 Nov. 6
	1955:	Jan. 23 Mar. 5, 6 May 17
Three	1954:	Oct. 5-6
	1955:	Jan. 3-4, Feb. 16-17
Four	1955:	March 17-18
Six	1955:	April 15-18

With the aid of the tidal records, an analysis of the degree of air exposure of the Upper level on Area 1 was made.*

Measurements on Area 1 indicated that the height of the upper level was 8.6 feet above Ordinance Datum, and that the vertical amplitude of the waves was 2.5 times that recorded by the tide gauge. The ability of the gauge to record waves was very important, since it was necessary to determine how long the level concerned remained dry. The gauge recorded the waves caused by the frequent steamer passages which would wet levels above high tide even on very calm days. Each such passage resulted in a series of waves lasting about one to two minutes.

The records from March 1954 to May 1955 were examined and all high tides which did not reach 8.6 feet were noted. These occurrences are given in Table 5.3. The only very long period of exposure during this time occurred in April, 1955, during the period of high mortality. The weather at the time was warm and calm, whereas during the long period of exposure in March it was cooler and rainy.

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* I wish to thank Mr. H. T. Powell, who provided the tide gauge records and the corrections to absolute height.

Table 5.4 --Maximum tide and wave heights reached in the period from April 15 to 19, 1955 (Feet above O.D.)

Date	Time	Average Height Of Tide	Ht. reached by Wind Waves	Waves Caused By Passing Steamer	
				Number	Height
Apr. 15	1740	8.6	8.8	1	9.1
" 16	0540	8.5	8.6	1	9.4
" 16	1835	7.9	8.1	2	8.9
" 17	0725	8.0	8.2	0	0.0
" 17	1957	7.9	8.2	1	8.7
" 18	0840	8.4	8.4	3	9.1
" 18	2110	8.5	8.5	1	8.7
" 19	0934	9.3	9.5	1	10.4

The period in April was investigated in detail, and the results are given in Table 5.4. The heights of the waves from the tide gauge records have been multiplied by 2.5. From April 16 at 0540 to April 18 at 2110 the level was untouched by any wind-driven continuous waves. In this time waves caused by steamers passing close to the shore wet the level six times, occurring in three of the four high tides.

This exposure of 60 hours with just six short wettings appears to have been fatal to many of the barnacles. Previous exposures of shorter duration did not cause such high mortality. It would probably be safe to say that no such long exposure had occurred in the past 2½ years, since no similar mortality had occurred on Area 2 or the Upper level of Area 1. In this locality the combination of calm warm weather and the very small amplitude of neap tides is evidently fairly rare.

At the high level of Area 2, the effects of these rare periods are probably the main cause of death for those individuals which survive the period immediately after settlement. The survival curves in Figure 13, indicate that very little mortality normally occurs after the first year of life so that accidents must be very rare; death from old age may occur in a few cases.

Since the unusual mortality of 1955 occurred within and just below the zone of Chthamalus, it may have provided space for a downward extension of Chthamalus in its autumn settlement. The settlement of Balanus in late April filled the existing spaces but the delayed detachment of dead individuals during the summer would probably provide more bare areas than in years when no such mortality occurred.

VI - Interrelations of the barnacles and the whelk predators.

This section is divided into two principal parts. The first is a description of certain studies of the feeding behaviour of Nucella lapillus. The second part is an analysis of the interaction between Nucella and the barnacle populations.

A. Feeding behaviour of Nucella.

1. Variations in feeding activity with tidal level and season.

a. Methods.

For indicating the positions of individual whelks, maps were made of Area 1 and Boulders 1, 2 and 6, showing the limpet positions and the cracks and irregularities of the rock surface. These maps were duplicated together on a single sheet and at each visit to the shore a new sheet was used to mark the whelk positions, using the limpets and mapped rock-irregularities as reference points.

For each month's records a calculation was made of the average number of whelks present per observation and was corrected to a square metre area so that comparisons between the boulders could be made.

Besides being at a different tidal level, the boulders had a very different barnacle population from Area 1. Area 1 always had some barnacles as food for the whelks, but the boulders were bare for the winter and spring of 1954 (Figure 10). For this reason therefore, it was felt that in comparing activity at different tidal heights, it was better to use levels within Area 1; this would also insure that wave exposure was similar between the areas compared. Area 1 was analyzed, the whelks which occurred at the various levels being counted separately. The three levels on Area 1, each 20 centimetres high as described previously, were counted, and in addition a 20 centimetre high strip above these. To compare the seaward and landward sides at the same level, each horizontal strip was divided into a north and south side and counted separately.

b. Variation of feeding activity with level.

The basic assumption underlying the method used was that whelks which were present on the open barnacle-covered rock were actively feeding. By slowly tilting a whelk away from the surface it could often be observed feeding on a barnacle, the opercular valves of which were gaping with the cirri partly exposed. Sometimes, especially with small barnacles, the whole operculum came away

Table 6.1 - The density of Nucella lapillus at various levels on Area 1.

Level	Mean density per 0.1 m.^{2}		"t" tests (performed on a log (x+1) transformation of the original data) of the significance of the difference between the mean densities								
	Seaward side	Landward side	Between levels, each side separately								Between sides at the same level
			Seaward side				Landward side				
			Mean	Variance	No. obs.	t	Mean	Variance	No. obs.	t	t
High	1.9	0.8	.307	.125	119	No test	.136	.063	119	No test	no test
Upper	4.7	3.8	.518	.168	123	6.06 **	.468	.133	123	0.35 NS	1.01 (N.S.)
Middle	4.8	3.4	.571	.111	123	5.05 **	.452	.128	123	0.83 NS	2.69 **
Lower	8.3	3.2	.788	.117	123		.489	.119	123		6.84 **

Note: Probabilities for judging significance are as follows:

Symbol	P	Judgment
NS	$>.05$	Not significant
*	$<.05$ $>.01$	Significant
**	$<.01$	Highly significant

on the whelk's foot. Of more than four hundred whelks examined in May, 1955, two-thirds were observed feeding; others were clinging to barnacles but not feeding. At all times of the year some whelks could be seen in crevices and among dense weed where there was little exposure to wave action, and may have been "resting". The non-feeding whelks on the open rock were probably searching for prey when exposed by the falling tide; some observations on this behaviour will be discussed later. However, the numbers observed are probably valid in comparisons of activity at different levels and in different seasons, even if some of the whelks were not actually feeding.

Above the "High" level, only 22 whelks were seen in 140 days observations in 19 months; ten of these were in December, 1954, seven in May, 1955.

A comparison between the different levels on Area 1 is made in Table 6.1. This vertical face of rock was oriented at about right angles to the shore. There was a decrease in density of Nucella with an increase in height on the seaward side, but this decrease occurred only at the high level on the landward side. There was also a decrease in density toward the landward side at

Table 6.2 -- Density of *Nucella lapillus*: (Number per m^2), averages of monthly means, excluding the months of January to June, 1954.

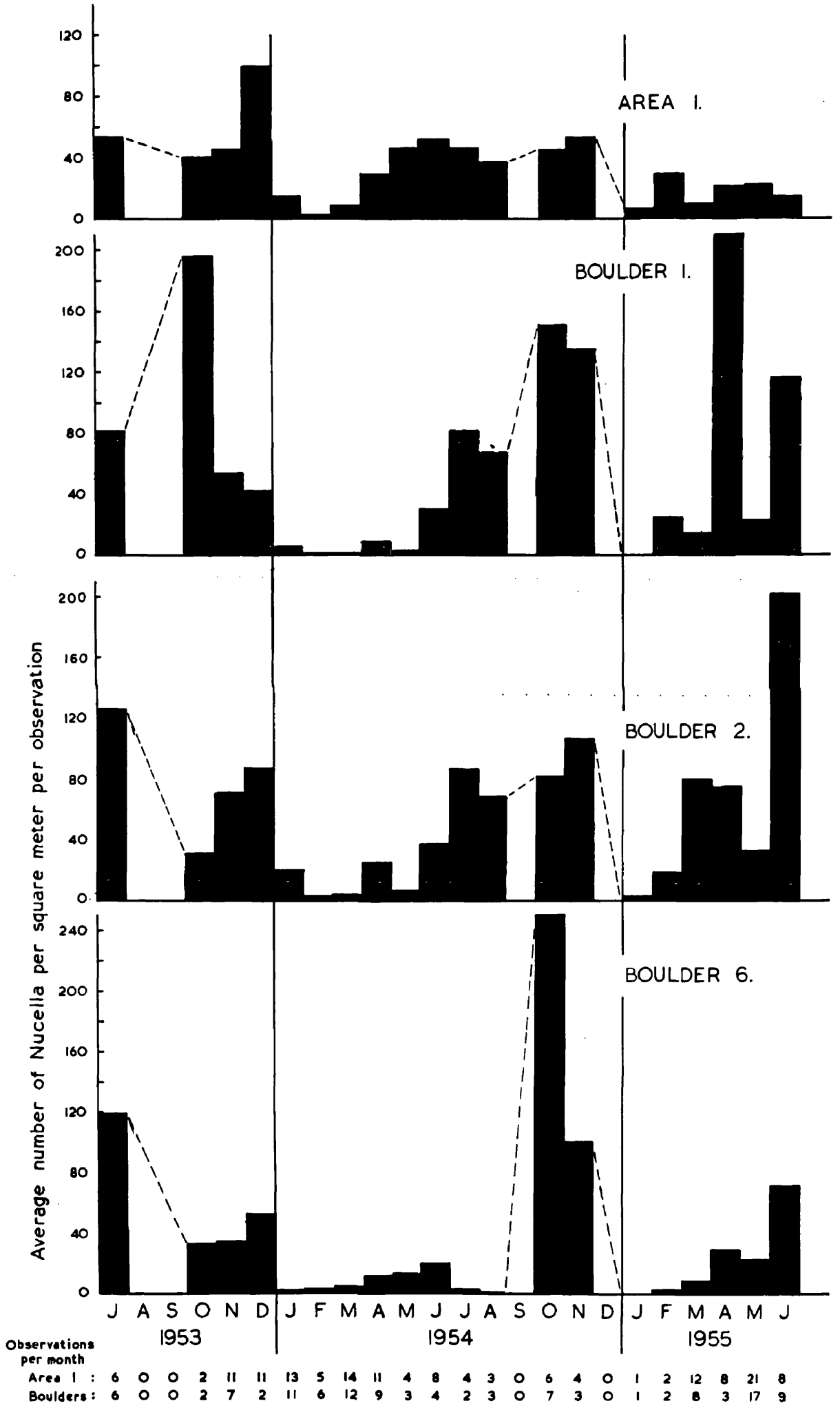
Area	Height in feet above or below MTL	Mean	No. of monthly means used.	Variance	t	Significance of difference, probability
Area 1, Low level only	+ 1.5	54.5	14	1571	1.24	> 0.2
Boulder 2	− 0.9	76.5	14	2503	0.47	0.5
Boulder 1	− 0.9	88.5	14	5480	1.11	> 0.2
Boulder 6	− 1.8	56.1	13	5040		

each of the two lower levels. While the decrease in numbers with height on the shore might be attributed to an avoidance by Nucella of long periods of exposure to air, the reasons for the horizontal differences are not known.

In Table 6.2, the densities of Nucella at the lowest level of Area 1 and on Boulders 1, 2 and 6 are compared. The number of observations in each month varied considerably so that to obtain an average density which would represent the whole period and be more comparable between levels, the monthly means, given in Figure 14, were averaged. Extreme variability is the most obvious characteristic of the data from the boulders. This variation was so high that even the large differences in the averages between the boulders and Area 1 might well have occurred by chance. It is evident from Figure 14, however, that at times the predation was much more intense on the low shore levels.

Few other records of counts of Nucella have been found. Moore, (1938b) in one observation in Skye in June, 1936, noted 200/m^2 just below .H.W.N. and 175/m^2 at MTL, the numbers decreasing above and below this to about 10/m^2. He states that Nucella "usually becomes less abundant some way below the top of the barnacle zone".

Figure 14. The average densities of Nucella lapillus for each month in which observations were made. The Area 1 data include all the levels within the area.


AREA 1.
BOULDER 1.
BOULDER 2.
BOULDER 6.
Average number of Nucella per square meter per observation
0
40
80
120
160
200
240
J A S O N D J F M A M J J A S O N D J F M A M J
1953
1954
1955
Observations per month
Area 1 : 6 0 0 2 11 11 13 5 14 11 4 8 4 3 0 6 4 0 1 2 12 8 21 8
Boulders : 6 0 0 2 7 2 11 6 12 9 3 4 2 3 0 7 3 0 1 2 8 3 17 9

Southward (1953) at two localities on the Isle of Man, gives counts which, when averaged, yield densities of 1.0 and 0.5 per m^2, with maxima of 31.0 and 12.0/m^2; all these Nucella were feeding on Balanus between the neap tide levels. The present records are somewhat higher than those of Skye. Very small whelks (less than 0.5 cm. in height) were found only below MTL, as noted by Moore (1938b).

c. Seasonal variations in activity.

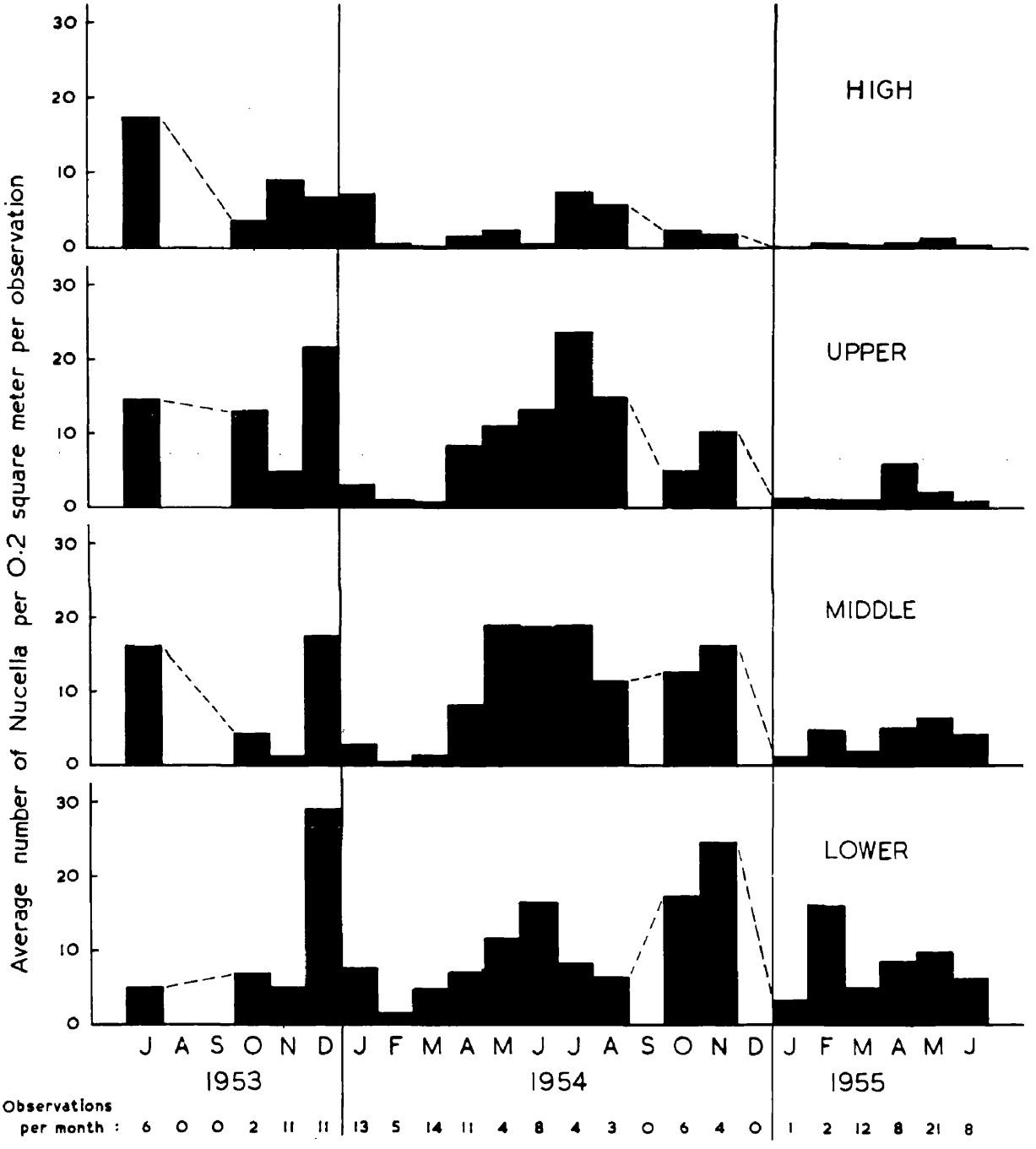
Figure 14 gives a summary of the monthly averages of density of whelks on the boulders and on Area 1 as a whole, from July 1953 to June 1955.

In both winters, a sudden drop in numbers began in January and continued through March on Area 1. No prey were available on Boulders 1, 2 and 6 in these months, 1954, but even in 1955 when barnacles were available there, the numbers were low. The density began to increase again in April, except on the boulders in 1954 when the new barnacle set did not arrive until May and feeding then began in July; some Nucella were present there in June, but were feeding on patches of Mytilus edulis.

A similar analysis of the four levels of Area 1, with seaward and landward sides of each level taken

together, is shown in Figure 15. After the low activity at the beginning of 1954, the density at the two lower levels increased to a peak in May and June. A decrease then occurred in the low level in the summer, while an increase occurred at the upper two levels. The records for the previous July showed a similar distribution. Few observations were made in late summer, but in December, 1953 and the late autumn of 1954, high densities occurred. More whelks were feeding at higher levels in the autumn of 1953 than in 1954. Some Nucella were noted feeding at low levels in the winter of 1955, but all these individuals were small individuals with thin shells. Moore (1936b) has shown that this type of shell indicates immaturity. In Moore (1938a) there is a diagram of seasonal changes in tissue weight of mature Nucella at Plymouth. The weight dropped during October, remained steady until January and then showed a large decline in February and March, beginning to increase again in April. He notes that immature whelks show no such winter drop in weight, and so ascribes the decrease in the weight of older individuals either to loss of reproductive products or cessation of feeding by the mature whelks during the main spawning period, January to April. From the present observations, the latter

Figure 15. The average densities in each month of Nucella lapillus on Area 1, each level given separately.


Average number of Nucellia per 0.2 square meter per observation
HIGH
UPPER
MIDDLE
LOWER
0
10
20
30
J A S O N D J F M A M J J A S O N D J F M A M J
1953
1954
1955
Observations per month : 6 0 0 2 11 11 13 5 14 11 4 8 4 3 0 6 4 0 1 2 12 8 21 8

seems more likely, since the few whelks seen feeding in the winter were immature individuals.

Various authors have noted the fact that whelks often retreat into crevices. Fischer-Piette (1935) regards this behaviour as being either an effect of extreme cold or a means of avoiding desiccation. Moore (1936b) considered that gales may limit feeding during the winter period when the tissue weight of mature whelks dropped but rejected this hypothesis since immature whelks showed no weight decrease at this time. It was noted on the present area that the whelks were in crevices not only after gales but also during a calm cold spell in January, 1955. Gales frequently occur at other times of the year, so that the pronounced low activity in late winter may more probably be ascribed to prevailing lower sea and air temperatures.

d. Proportion of population feeding.

Even during times of intense activity some whelks were found among dense weed or in crevices. To discover what proportion of the population was feeding at any one time, some data collected from individually marked whelks in July, 1953, were analyzed. The marking was done with Indian ink, the numbers being protected by a transparent film of Distrene dissolved in xylol as described by

Table 6.3 -- The proportion of the *Nucella* population feeding at any one time.

July, 1953

Date:	18	19	21	22	24	25	26	27	28 early tide	28 late tide	Total
Total No. of *Nucella* observed on this date or at a later examination:	37	35	82	82	81	81	80	79	79	78	714
Total No. observed on this date only (= number feeding):	21	23	47	44	36	51	35	37	37	45	376
Percentage feeding each day:	59	66	57	54	44	63	44	47	47	58	53

Note: See text for explanation.

Quayle (1952). (One whelk was recovered 22 months after marking with the number still intact).

During two low tide periods ninety whelks were marked. During the next twelve days their presence among barnacles on the open rock was noted at seventeen low tides. Any not visible on the open rock but noted at a subsequent observation were assumed to be "resting" at the time. A reasonable number of later observations was needed to make sure that missing individuals in the early records were simply "resting" and had not died or moved to another area; for this reason only the first eight of the seventeen observations were used to compute the percentage of marked whelks which were feeding at each observation. Any of the originally marked individuals which did not reappear in a later observation were not used in the calculation. The results are given in Table 6.3. The overall figure of 50% is probably too low, since the assumption that missing whelks were necessarily not feeding is probably not completely true. Another calculation from observations during nine successive low tides on an adjacent area gave the value of 66% feeding per observation. These few observations suggest that even during the warm part of the year only from one-half to two-thirds of the population was feeding at one time.

Individual whelks showed a great variation in the lengths of their feeding periods. In the observations during nine successive low tides, two individuals were noted at every tide, and two more for seven and eight successive tides each. For the thirty-one individuals noted, the average number of successive low tides that a whelk remained feeding was 3. On the average, therefore, in the summer a whelk fed for about three successive tides and then "rested" for about two tides before beginning to feed again.

2. The feeding rate of Nucella.

a. Methods.

Two methods were used to determine the rate of feeding by Nucella. The first consisted of calculating the difference in mortality between caged and unprotected barnacle populations on Area 1; this difference was taken to be the number eaten by Nucella. Knowing the average number of whelks present, from the previously described census method, the numbers of barnacles presumably eaten per day by one whelk could be calculated. This method will be referred to as the "exclusion method."

The second method was to place a whelk inside a cage and count the barnacles at intervals. An adjacent

empty cage gave the deaths from other causes. This will be termed the "enclosure" method.

Since the object was partly to determine the causes of any variations in feeding rate, the seasons were considered separately. The exact intervals are given in Tables 6.4 and 6.5; these were selected to represent periods of greater and lesser activity of Nucella, based on the variations shown in Figure 15.

The exclusion method was carried out as follows at each level of Area 1. The percentage of deaths over the interval was calculated for each age group separately on the protected area. This percentage was then multiplied by the number in the particular age group in the unprotected population to give the number of deaths from causes other than predation. The difference between this number and the total death in the unprotected population was assumed to be caused by predation. The number killed per unit area per day was then calculated, and divided by the average number of whelks noted per unit area per observation. The density of whelks used was that calculated for the 1/10 square metre which contained the barnacle area being considered and comprised one side of the particular 20 cm. high horizontal strip described in the previous section.

Enclosure of a whelk in a cage was carried out in four separate experiments.

Experiment 1.--July 22nd to August 8th, 1953, at MTL. The barnacles were very dense so all dead individuals were removed and at the next inspection only dead barnacles were counted. After the second weekly inspection it was decided to abandon this experiment since many deaths were occuring in the control cage, probably as a result of extreme crowding.

Experiment 2.--September 10th to December 11th, 1953, below MTL. Here the barnacles were scattered and complete counts were made at each examination. Two cages were used, one with a single large Nucella in it, until October 21st; after this two more cages were attached with a Nucella in each. In December many very small Nucella began entering the cages so the experiment was ended.

Experiment 3.--November 11th, 1953 to August 8th, 1954. Four cages were attached at the Middle level of Area 1, about one foot north of Cage 1. Two had one whelk each, two were kept as controls. These were $\frac{1}{4}$" mesh cages, but the absence of small whelks above MTL rendered this large mesh satisfactory.

Table 6.4 - The feeding rate of Nucella lapillus: a. Exclusion of whelks from caged areas on Area 1. as compared to natural areas.

Level	Area	Number of barnacles eaten by one Nucella in one day in the following periods: Autumn Oct.-Dec. 1953	Winter Jan.-Mar. 1954	Spring Apr.-June 1954	Autumn Oct.-Dec. 1954	Average of whole period
Upper	Cover	2.4	2.0	3.0	(10.7)	2.5
"	Control 1.	3.1	6.7	3.5	(33.1)	4.4
"	Control 2.	2.4	0	-	-	1.2
"	Control 3.	-	-	-	4.9	4.9
"	Average	2.6	2.9	3.3	4.9	3.1
Middle	Cover	0	0	2.3	1.1	0.8
"	Control 1.	1.7	1.2	1.4	0.2	1.1
"	Control 2.	(13.2)	0.4	1.5	3.1	1.7
"	Average	0.8	0.5	1.7	1.5	1.2
Lower	Control 1.	1.7	1.8	2.4	2.1	2.0
"	Control 2.	-	3.9	3.0	0.8	2.6
"	Control 3.	-	5.1	3.1	2.5	3.6
"	Average	1.7	3.6	2.8	1.8	2.6
Area 1. Average		1.9	2.3	2.5	2.1	2.2

Note: The values in brackets were not included in the calculations of the average figures.

Experiment 4.--October 22nd, 1954 to May 31st, 1955. Five cages were attached to a slightly sloping rock face five yards east of Area 1 at the height of the "Lower" level of Area 1. Two whelks were placed in each of three cages, four in another cage and one cage was kept as a control. One of the "two-whelk" cages contained only 6 months-old barnacles as prey while the other four cages contained three year-groups. In the last two months of this experiment the mortality in the control cage began to increase. This was probably due to the increase in crowding as the barnacles began their spring growth. However, the barnacles in other cages, having been "thinned out" by predation, experienced little crowding. Thus there was no adequate measure of the mortality from causes other than predation taking place in the cages with whelks in them for the spring period.

b. Results.

The feeding rates calculated from the exclusion method are given in Table 6.4. Some of the values have been placed in brackets since they seemed excessively high. These high values may have resulted from damage from water-borne objects. The two "cover" squares were protected from such damage and their rates are about 25%

Table 6.5 - The feeding rate of *Nucella lapillus*. b. Whelks enclosed in cages with barnacles.

Experiment No.	Inclusive Dates	Density and age of the barnacle population	Length of whelk in cm.	Average number of barnacles eaten by one *Nucella* in one day in the following periods		
				Autumn Sept.-mid-Dec.)	Winter (mid-Dec.-March)	Spring and summer (April-Aug.)
1.	July 22-Aug. 8, 1953	Very dense, 3 mo. old	2.0	-	-	2.0
2.	Sept. 10-Dec. 11, 1953	Scattered barnacles, 6-8 mo. old	2.8 2.1 3.1	2.6 2.1 0.8	-	-
3.	Nov. 11, 1953 to Aug. 8, 1954	Moderate density, 3 year groups of barnacles	not meas.	1.3 (older 1.0 young 0.3)	0.3 (older 0.2 young 0.1)	1.6 (older 1.5 young 0.1)
4.	Oct. 22, 1954 to May 31, 1955	Moderate density, 3 year-groups (cages 1,2,5)	Six whelks, 2.3-2.7	1.0	0.4	-
		6-13 mo. group only (cage 4)	Two whelks, 2.6, 2.8	1.3	0.4	-

Note: In experiment No. 3, the "young"barnacles referred to were seven months old at the start of the experiment. None of the 1954 settlement were eaten.

below the average for the same level. However the high mortality on the Upper cover square in the autumn of 1954 cannot be explained by damage. The most likely explanation is that more predation was occurring than the observations indicated. Whelks often feed in groups, and if such an aggregation was missed in the whelk counts, the numbers of predators would have been underestimated. An analysis of variance of these data, given in Table 6.6, showed that the seasonal variation in rate of feeding is less than that observed between the observations in any one season although the latter difference was small and was judged to be not significant.

The results of the experiments with whelks enclosed in cages are given in Table 6.5. These yielded much less variable results, probably because the number of predators was known exactly, and damage was prevented. In contrast to the previous method, the rates of feeding were much lower in the winter. For each cage of Exp. 4, the average area covered by individual barnacles in each year class was measured from photographs with a planimeter. This was done since it appeared that the older barnacles were larger in two of the cages than in the others. The feeding rates were re-calculated as area of barnacles

Table 6.6 - The feeding rate of Nucella lapillus.
c. Analyses of Variance of the original data used to compute the values in Tables 6.7 and 6.8.

(1.) Exclusion experiments, Table 6.7.

Source of variation	Sum of squares	d.f.	Variance estimate	F	p
Between seasons:	1.6	3	0.53	5.11	>.05
Within seasons :	70.5	26	2.71		
Total :	72.1	29			

(2) Enclosure experiment 4, Table 6.8, numbers of barnacles.

a. Cages 1, 2, and 5. Three age groups of barnacles.

Between seasons:	144.5	1	144.5	6.23	<.05 >.01
Within seasons :	417.5	18	23.2		
Total :	562.0	19			

b. Cage 4, young barnacles only.

Between seasons:	129.2	1	129.2	8.91	<.05 >.01
Within seasons :	72.5	5	14.5		
Total :	201.7	6			

(3.) Enclosure experiment 4. Areas of barnacles, all cages.

Between seasons:	664	1	664.0	9.85	<.01
Within seasons :	1685	25	67.4		
Total :	2349	26			

Note: The probability "p" was obtained from the variance ratio "F" distribution tables. Values of p less than .05 were judged to be significant.

eaten. Analyses of variance of these data, given in Table 6.6, showed a significant seasonal variation as compared to the variation between the observations in each season.

The different values obtained by the two methods require some explanation. The rates obtained for whelks enclosed in cages were much lower, even as compared to the cover squares of Area 1 where little damage occurred. In the marking experiments it was shown that whelks only feed about half to two-thirds of the time in summer. In calculating the feeding rates of the enclosed whelks the total time between observations was used; this included periods when the whelk was not feeding. On the other hand, in the exclusion method only whelks active on the rock among barnacles were used for the calculation and so the periods of non-feeding were not included. If the whelks in the cages fed only about half the time, the resulting rate would be about half that calculated by the exclusion method. This was about the difference observed between the rates calculated from the exclusion method and from Experiments 3 and 4 in the enclosure method. (Experiments 1 and 2 were performed lower on the shore with only young barnacles present, so are not strictly comparable with the results of the exclusion method.)

Besides the differences in magnitude of the rates calculated by the two methods, a difference in seasonal variation was found. The enclosed whelks had low feeding rates in winter, but the exclusion method yielded rates as high in winter as in other seasons. One explanation might be that the high rates shown by the exclusion method in winter were due to higher death rates of the barnacles caused by increased damage in winter. If this is so, areas protected from damage should have shown a decrease in death rate of about the same magnitude as that found in the enclosure experiments. But the protected Upper cover square showed only a slightly lower rate in winter while there was apparently no predation on the Middle cover in autumn or winter. Therefore it does not seem likely that extra damage in winter would raise the death rate of the barnacles to the extent of masking a drop in the feeding rate of Nucella.

The exclusion method might have given higher feeding rates in the winter for another reason. It has been pointed out that most of the whelks feeding in winter were immature. If these feed somewhat faster than the older ones, the average winter rate would be apparently higher simply because the older whelks were

not included. The only evidence available on this point is given in Table 6.5, experiment 2. The largest whelk did eat less than the other two, although the second largest ate most. It does not seem likely that this would account for the observed difference between the results of the two methods, however.

The fact that fewer numbers of whelks were seen on the open rock in winter (Figures 14 and 15) probably indicates that they spend much more of their time resting between feeding excursions. Thus, the slowing of feeding rate in winter shown by the enclosure experiments can be explained by the fact that the whelks rested proportionately longer in winter. The exclusion experiments showed that when the whelks were actually feeding they accounted for almost the same number of barnacles per day in the winter as in the summer.

B. Observations of the barnacle population under varying degrees of predation.

1. Experimental Area 1.

a. Effectiveness of the exclusion cages.

Occasionally small Nucella, ½ to 1 cm. in length, entered the cages through gaps at the line of juncture of netting and rock surface. These gaps were probably caused by distortion of the cage in strong wave action

or from crumbling of the rock. Since inspections were frequent and the likelihood small of a whelk escaping back through the gap, it is believed that all these entries were noted. To indicate the extent of these lapses in predator control, each occurrence was multiplied by half the time since the last inspection. Summing these times for all occurrences and dividing by the total time of attachment of the cages yields the value of 1.3% as the proportion of time of small whelk predation inside the cages. Since the cages gave complete protection against medium and large sized Nucella, the method can probably be judged effective. With infrequent inspections, modifications would be necessary.

Very small Nucella, able to pass directly through the 1/8" mesh, were not recorded on Area 1, although their abundance low on the shore rendered ineffective there all attempts at control by cages.

Only one instance of human interference occurred, in July, 1954, when the Upper Cage 1 was removed in the author's absence. A new cage was attached after twelve days of predation; the effect can be seen in Figure 16.

Besides excluding the whelks the cages gave protection from damage by water-borne objects. This protection completely altered the appearance of the barnacle

population. In the two cages which were in place for 2½ years, barnacles of succeeding settlements attached to surviving adults and grew higher, sometimes bridging the spaces between the older individuals. Examples of this are illustrated in the series of photographs in Figure 19. These populations resembled the clusters of sublittoral barnacles such as Balanus balanus (Barnes, 1953b) where three year-groups may be attached to one older barnacle. This condition did not exist on unprotected areas of Balanus balanoides even above the range of Nucella predation probably because the uppermost barnacles would be very vulnerable to damage.

Since this situation was so different from the normal one outside the cages, new caged squares were established at intervals, beginning a year after the first cages had been attached. These resembled the natural areas closely for at least a year or more following their enclosure. With frequent visits and the addition of new cages at about yearly intervals, this method of predator control was very satisfactory. Some algal fouling on the cages occurred, especially by Porphyra umbilicalis; it was easily removed and constituted no problem. This fouling was much heavier on other cages attached below MTL. Limpets were placed

Figure 16. The survival of Balanus balanoides with and without predation by Nucella lapillus on Area 1, Upper level. Only those barnacles attached directly to the rock surface have been included. The heavy lines indicate areas protected from predation inside cages, the thin lines, unprotected natural areas. In cage 1., the broken portion of the line indicates a twelve day period when the cage was missing and intense predation occurred, in July, 1954.

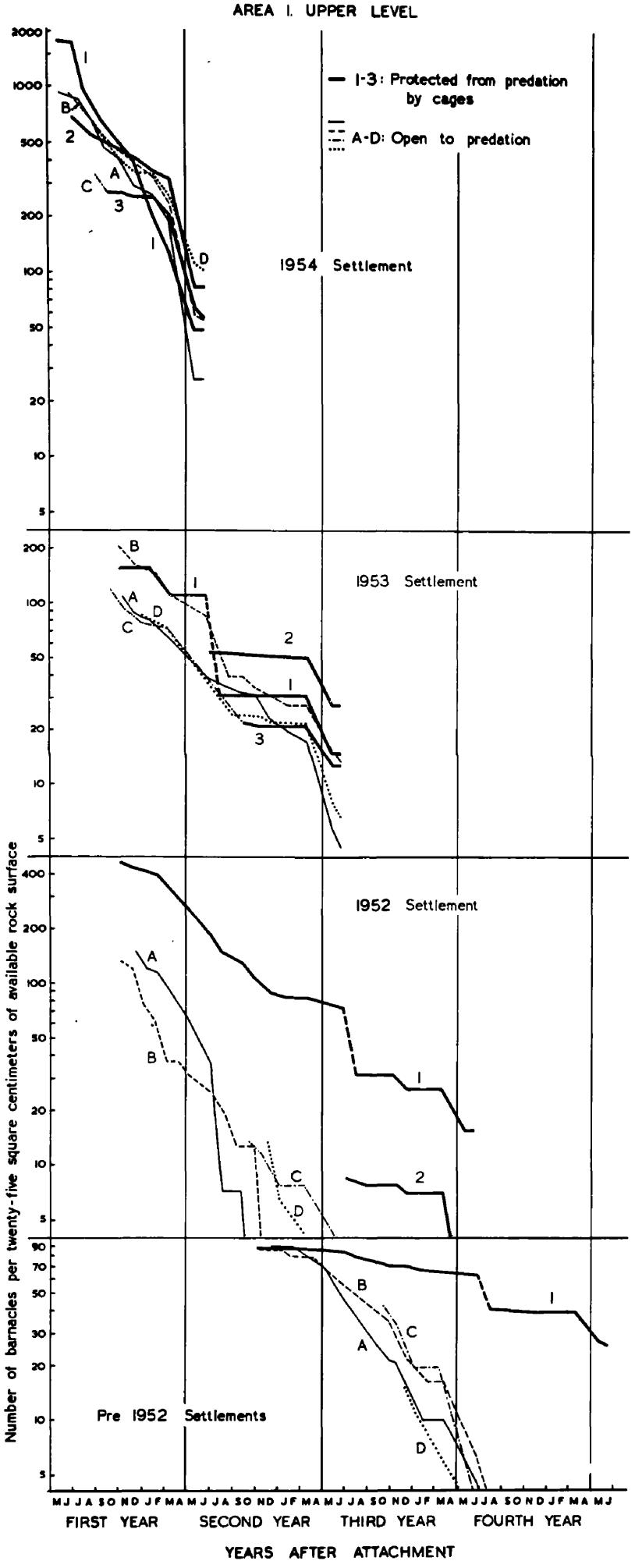

AREA I. UPPER LEVEL
1-3: Protected from predation by cages
A-D: Open to predation
1954 Settlement
1953 Settlement
1952 Settlement
Pre 1952 Settlements
Number of barnacles per twenty-five square centimeters of available rock surface
2000
1000
500
200
100
50
20
10
5
400
90
70
50
30
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
FIRST YEAR
SECOND YEAR
THIRD YEAR
FOURTH YEAR
YEARS AFTER ATTACHMENT

Figure 17. The survival of Balanus balanoides on Area 1, Middle level. The thick lines denote populations in cages protected from predation; the thin lines indicate natural areas, not protected.

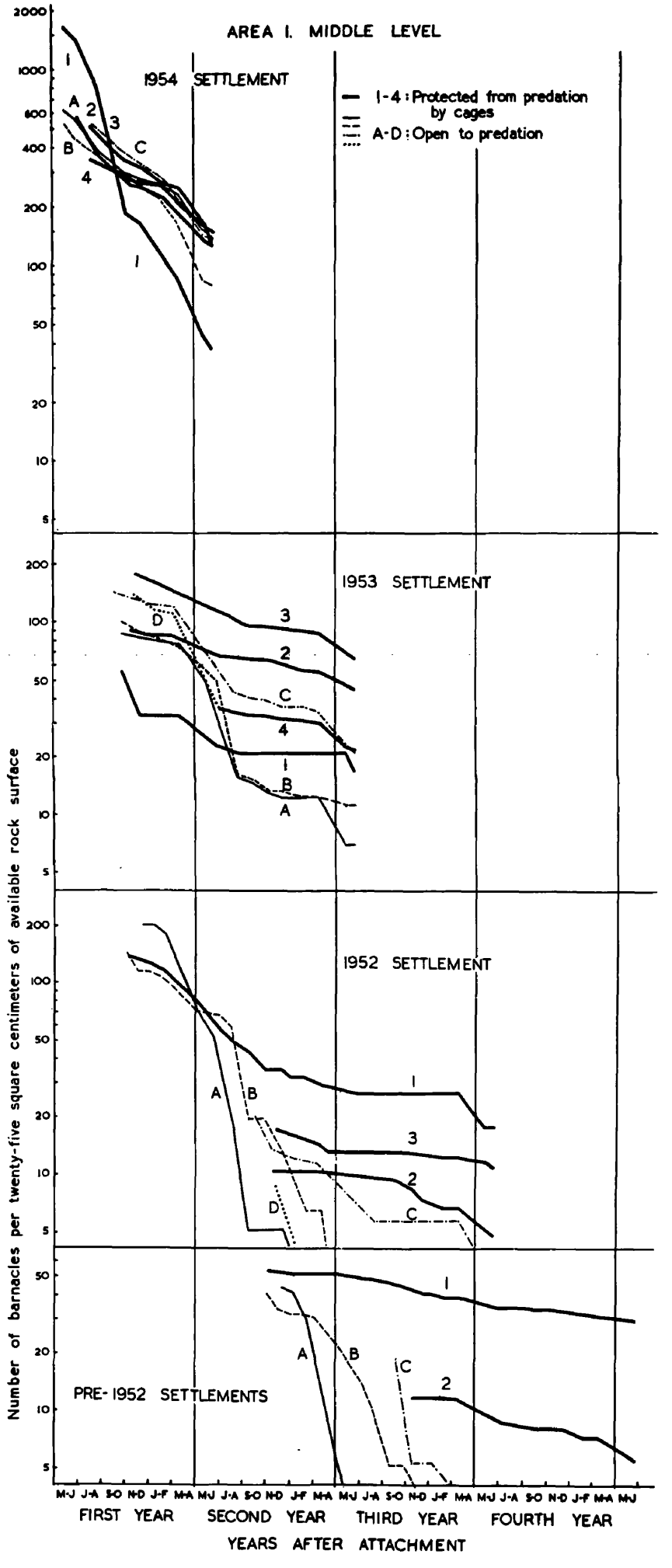
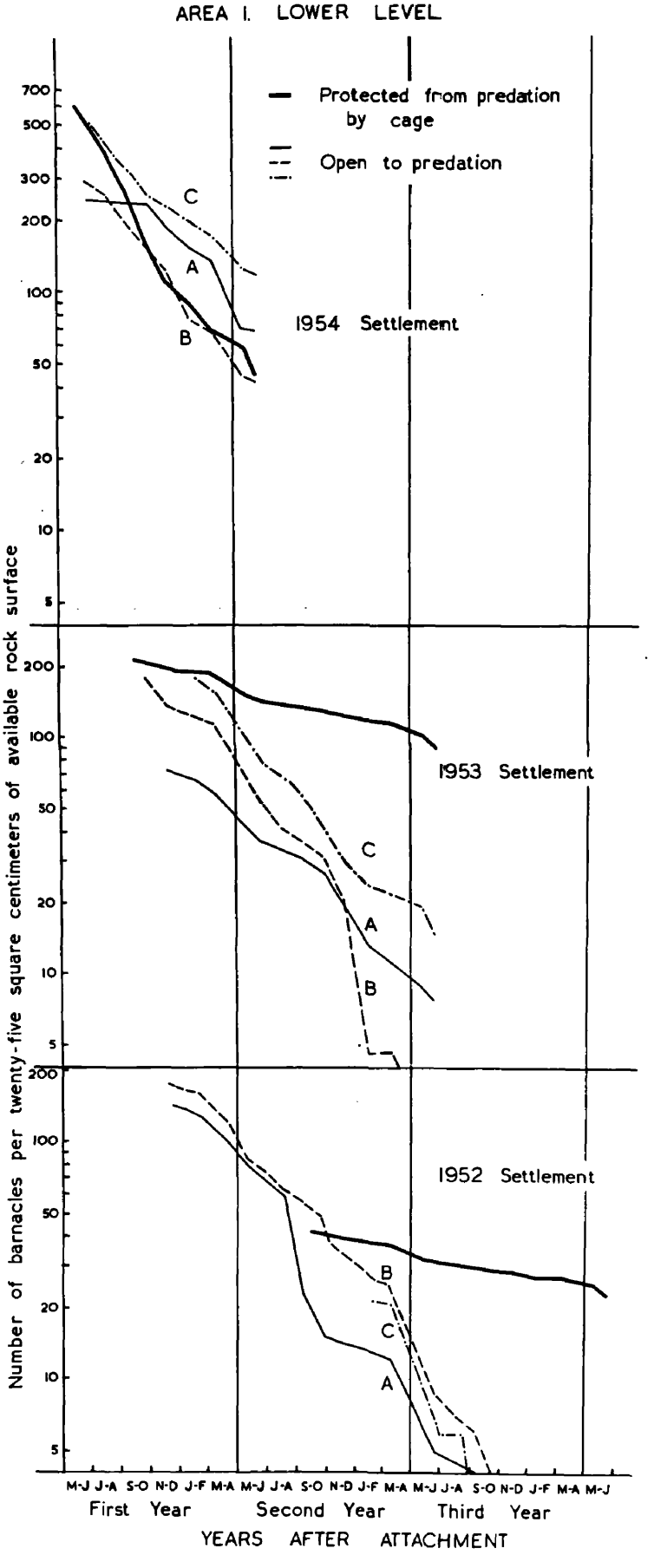

AREA I. MIDDLE LEVEL
1954 SETTLEMENT
1-4 : Protected from predation by cages
A-D : Open to predation
1953 SETTLEMENT
1952 SETTLEMENT
PRE-1952 SETTLEMENTS
Number of barnacles per twenty-five square centimeters of available rock surface
2000
1000
600
400
200
100
50
20
10
5
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
FIRST YEAR
SECOND YEAR
THIRD YEAR
FOURTH YEAR
YEARS AFTER ATTACHMENT

Figure 18. The survival of Balanus balanoides at the Lower level, Area 1. The thick line denotes a population in a cage, protected from predation; the thin lines indicate natural areas.


AREA I. LOWER LEVEL
Protected from predation by cage
Open to predation
1954 Settlement
1953 Settlement
1952 Settlement
A
B
C
700
500
300
200
100
50
20
10
5
Number of barnacles per twenty-five square centimeters of available rock surface
M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J J-A S-O N-D J-F M-A M-J
First Year
Second Year
Third Year
YEARS AFTER ATTACHMENT

inside the cages in the summer of 1953 to control the growth of algae which had begun to grow abundantly in the cages.

b. Results of the exclusion experiments on Area 1.

Figures 16 to 18 show the survival of barnacles on all the squares counted at each of the three levels of Area 1. The density is indicated by the height of the curve, the relative death rate at any time by the slope. The relation of mortality to density in the early growing stages has been discussed in section IV. A comparison of the slopes of the survival curves of caged and uncaged areas indicates that predation is a minor factor in causing the mortality during the first year above MTL; this was also illustrated in Figure 8. The slopes first begin to diverge at the end of the first year; the unprotected populations then experience an increase in relative death rate, while that of the protected ones either remains constant or decreases. The highest death rate due to predation, (indicated by the greatest differences in slopes of the two types of curves), occurs in the summer. It slackens in September at the Upper and Middle levels in the second year of life, but continues high through the autumn and early winter in the older groups at these levels and in all

Figure 19a. The effects of protection by cages, as shown by Middle Cage 1 and the adjacent Middle Control 1. The cage was attached about 3½ months before the first photograph was taken. (Scale x 0.6 to 0.8)

February 22, 1953

February 3, 1954

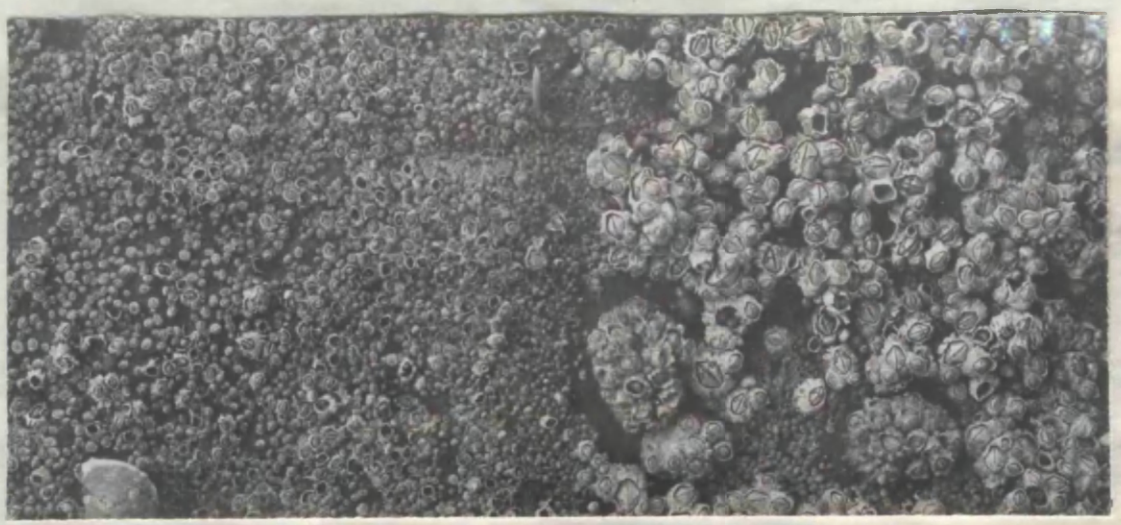
February 18, 1955

Middle Control 1.

Middle Cage 1.

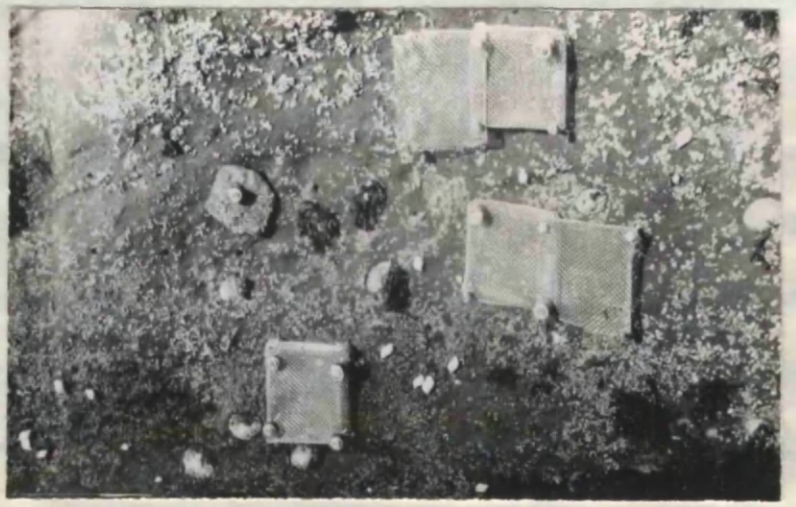
Figure 19b. The same areas as in the preceding figure, but shown just after the new settlement had finished. Also shown is a general view of Area 1, x 1/10.

June 27, 1954



June 9, 1955

Middle Control 1. Middle Cage 1.



Area 1, April 6, 1954

ages at the Lower level. These variations are coordinated with the seasonal variations in the activity of Nucella, as shown in Figure 15.

2. The effect of predation on the barnacle populations on other areas of the intertidal zone.

The variation in age structure of the barnacle population at different shore levels on the area studied is similar to that described by Moore (1934) for the Isle of Man. Above the level of Area 1, near HWN, the population consists mainly of large older individuals. Below MTL, the proportion of the older age groups dwindles, until near LWN only the most recent year class is present except for a short period of overlap in the spring when the survivors of the previous year are mixed with the newly settled group. Figure 10 illustrates the survival on Boulders 1, 2, 5 & 6, below MTL.

When the density was low on these areas, and crowding was not intense the relative mortality rate was closely correlated with the abundance of predators. On Boulder 6, in 1954 (Figure 10), the relative mortality rate increased greatly during October and November and then decreased. At the same time, as can be seen in Figure 14, the numbers of Nucella increased and decreased. The same correlation is shown on Boulders 1 and 2 in the autumn of 1954 and the spring of 1955.

3. Variation in the age at which predation begins.

On Area 1, it was seen that the death rates for the first year of life were not related to predation. Lower on the shore, where growth is much more rapid and the new set constitutes the main proportion of the barnacle population, predation begins much sooner. In 1954, Boulders 1, 2 and 5 were bare before settlement so that a completely new set occurred at low level. Nucella were first observed on these boulders after July 10 when the barnacles were about 8 weeks of age. In 1955, boulders at various levels were scraped clean a month before settlement. These received their first settlers at the beginning of April; whelks were first observed feeding on the lower of these areas, adjacent to Boulders 1 and 2, on May 11, when the barnacles were only 5 to 6 weeks old. On similarly treated areas above MTL no feeding by Nucella occurred.

The difference between the two years in the age at which predation began may possibly be explained by the differences in distribution of Nucella. In Figure 14 it is shown that many fewer Nucella were present on Boulders 1 and 2 in May and June of 1954 than in these months in 1955. Also, there were adult barnacles present

on these areas in 1955 but not in 1954 (Figure 10). It appears that the presence of adult barnacles attracted large numbers of Nucella, which then began to feed on the newly settled barnacles. In the following discussion it will be demonstrated that Nucella does tend to feed more on adult barnacles so that the presence of adults would be expected to attract more Nucella.

Fischer-Piette (1935) noted that Nucella did not attack Balanus balanoides until six months after attachment; no indication of shore level is given, however.

4. Evidence of selection of larger sized barnacles by Nucella.

If a Nucella feeds whenever it is "hungry" on the barnacle it is then touching, it would be expected to encounter and feed most on the group which covers the greatest proportion of the surface area. From this hypothesis, some feeding would be expected to occur on the newly settled group on Area 1. Since this did not happen, it must be concluded that the whelks ignored this young group and selected older individuals. These older barnacles, besides being larger, had rough shells, the upper edges of the wall and opercular plates being worn and rounded. This may have enabled Nucella to distinguish older individuals.

Besides this evidence of selection some direct observations were made in a simpler situation where only two age groups were present. In May, 1955, it was noted that some Nucella were feeding between MTL and LWN on the new set when it was 5-6 weeks old. Some were feeding also on survivors of the previous years, although these comprised only a small proportion of the total barnacle cover. The Nucella thus had two groups of contrasting sizes to choose from. The proportions of the area occupied by old and young barnacles were determined by laying a metre square frame divided into 100 $cm.^{-2}$ squares on the rock, and, for each square separately, estimating by eye the total barnacle cover, the coverage of the older group (their yellow shells contrasted well with the background) and the percentage of these older barnacles which were alive. By estimating each small square independently it was felt that a very close approximation to the true proportions could be made. On each rock area, one horizontal and two vertical transects were made of ten such squares. Since at this stage very few young were dead, the coverage of living young ones was calculated as the total barnacle cover minus the coverage of older barnacles. This estimate of older barnacles included both dead and live individuals, and so it was multiplied by the percentage

alive to give the area of living older individuals. The proportion of live old to live young was then calculated. Since some young which had settled inside the dead adult shells were missed and some adults killed by Nucella still had their opercular plates in place, it was felt that the error in the measurement tended to overestimate the proportion of living adults.

On the assumption that no selection between the two groups by Nucella was taking place, it would be expected that the distribution of Nucella actually observed feeding, would occur in proportion to the area covered by each age-group of barnacles. To test this hypothesis, on these areas each Nucella was carefully tilted away from the surface to expose the individual barnacle upon which it was feeding. When a Nucella was feeding on a barnacle the opercular valves were usually opened out, with a white "cleaned" spot at the juncture of the valves. This spot appears to be made by the whelk in the process of opening the barnacle. Since it occurs in both old and new barnacles, it made the identification of the individual being eaten equally certain in both groups. In some instances the Nucella was attached to the rock surface or to an individual barnacle which showed no sign of being attacked. These instances were noted as indeterminate, and were not used in the calculations.

Table 6.7 -- The observed numbers of *Nucella* feeding on each age group and the expected numbers, calculated from the total numbers on the assumption that the *Nucella* occurred on each group in proportion to the area covered by it.

	Observed and expected numbers of *Nucella* for each daily observation.						Total Numbers	
	May 18 Obs.	Exp.	May 19 Obs.	Exp.	May 20 Obs.	Exp.	May 21 Obs.	Exp.	May 22 Obs.	Exp.	May 24 Obs.	Exp.	Obs.	Exp.
No. of *Nucella* feeding on one year old barnacles:	49	12	28	8	25	6	30	7	36	9	28	8	196	49
No. of *Nucella* feeding on newly settled barnacles:	10	47	11	31	6	25	8	31	9	36	11	31	55	202
Total *Nucella* Observed:	59		39		31		38		45		39		251	
Chi-square	151.5		67.9		74.6		85.7		101.2		67.9		549.0	
Probability:	< .001		<.001		<.001		<.001		<.001		<.001		<<.001	

The results of these observations are given in Table. 6.7.

The total number of Nucella which were feeding each day was also divided into the proportions of the areas occupied by the two barnacle groups, as expected on the assumption that there was no selection. By comparing the expected and observed distributions with the chi-square test, it can be seen that the probability of such a distribution arising by chance is very low, and that selection almost certainly took place, the whelks choosing the adult barnacles.

Some areas, adjacent to those just discussed, having been scraped clean before the 1955 settlement began, were covered only by young newly settled individuals. The whelks feeding on these individuals, which were then 5 to 6 weeks old, seemed from casual observation to be eating the larger of these barnacles. To test this observation, on these areas each Nucella was lifted as before and the individual being eaten was identified and measured. On the same day a piece of the rock was chipped off from the same area and was brought into the laboratory where all the individuals on a small area were measured to indicate the size variation in the total prey population. The results of these measurements from two nearby areas are given in Table 6.8. It can be seen that not only the average size, but also the size range

Table 6.8 -- The size of individuals of *Balanus* eaten by *Nucella* from a barnacle population consisting of only the 1955 settlement at an age of about six weeks.

Date		Length of *Balanus*: No. measured	Mean length mm.	Size range mm.	Variance
May 17-18	Total Population.	103	2.0	0.9-3.1	0.39
	Individuals being eaten.	44	2.6	1.7-3.2	0.14
May 20-21	Total Population.	50	2.5	1.0-3.7	0.59
	Individuals being eaten.	21	3.0	2.5-3.7	0.15
May 23-24	Total Population.	50	2.5	1.0-3.7	0.59
	Individuals being eaten.	40	2.9	1.9-3.8	0.19

of the group being eaten lies mostly above the mean size of the total population, indicating a choice of the larger individuals by Nucella. Since these were not apparently rougher or more eroded than the smaller individuals, size alone seems to be the stimulus to the whelk. Large barnacles in a dense settlement tend to stand apart as individuals in comparison to the many average-sized individuals around them, and this may create a spatial discontinuity acting as a tactile stimulus to Nucella. This situation is illustrated in Figure 4.

Some data collected from marked whelks in July 1953 showed that some movement occurred at almost every tide. Most of this was probably a searching for prey. Marking experiments could only record the movements of individuals which remained on the open rock for at least two successive tides, and probably tended to record more data from individuals which fed for longer periods, missing any greater movements into crevices or weed. However, the records are probably fairly representative of movements during feeding. The results of a series of observations over nine successive tides are given in Table 6.9. In the 114 observations, six whelks were apparently in the same spot as at the previous low tide and the median distance moved was only 4 cm. It appears

Table 6.9 -- Movements of marked Nucella observed over nine successive tides; distances given in cm.

Date (July - Aug. 1953)	29	30	30	31	31	1	1	2	Total
No. Nucella observed	12	16	15	17	13	14	14	13	114
Sum of distances moved by all Nucella	49	56	117	202	110	137	88	71	830
Average distance moved by one Nucella in one high tide	4.1	3.5	7.8	11.9	8.5	9.8	6.3	5.5	7.3

Note: For each whelk whose movements were observed more than once an individual average was calculated. These averages showed a range of from 1.0 to 21.7 cm.

The greatest movement recorded was 37 cm., and the median measurement was 4.3 cm.

that on an area of almost continuous barnacles, the feeding whelks do not simply move from one barnacle to the next, but probably touch at least ten to thirty barnacles, (assuming straight line distances and about four barnacles to a centimetre), while they eat an average of three barnacles a day.

The relation of the size of a whelk to either the size of its prey or its rate of feeding appears to be very irregular. In Enclosure Experiment 2, the whelk 2.1 cm. long ate much more than the one 3.1 cm. long, but this is the only evidence available on this aspect. In the observations on size selection reported in Table 6.8, the size of some of the whelks was measured at the same time as that of the barnacles being fed upon. The average size of the 55 whelks measured was 27.1 mm., all but nine being between 25 and 30 mm. The average length of the killed barnacles was 2.9 mm. The very large or small whelks showed no consistent relation to the size of their prey. A scatter diagram of size of whelk vs. size of the barnacle it was feeding on showed no trend, but only a cluster of points near the average sizes of the two animals. The extreme individuals showed irregular behaviour.

Two whelks which were much smaller than the rest (6.5 and 8.5 mm.) were feeding on 2.0 and 2.8 mm. barnacles, respectively, whereas one exceptionally large whelk of 37 mm. was eating a 3.2 mm. barnacle. The largest and smallest barnacles (1.9 and 3.8 mm.) were being eaten by whelks of 29 and 28 mm., respectively.

One other aspect of whelk behaviour which might have a bearing on the selection of larger barnacles is the habit-forming behaviour described by Fischer-Piette (1935). Fischer-Piette described how the whelks had difficulty in changing their food from barnacles to mussels. The mus sels were usually drilled through but barnacles were only rarely drilled. In the present study a few barnacles have been found drilled through one opercular valve or, once, through the side wall; these were in a cage below MTL in which only very small whelks were present. Apparently the opercular valves are opened in the same way as the barnacle opens its own valves, that is to say, outward. As pointed out earlier, barnacles which have been opened by Nucella usually show a small white area at the juncture of the two opercular valves, which is formed by the removal of the outer layer of shell (probably by the radula) so that a smooth "cleaned" spot remains. This is never drilled through, even in very

small new barnacles, and suggests that such a cleaned spot may afford a better contact for some type of attachment, such as a sucker, the valves then being pulled outward while the rest of the foot adheres to the outer shell of the barnacle and surrounding surfaces. Direct observation is almost impossible except by the method described earlier of tilting the whelk slowly away. Fretter (1946) has described a sucker in the anterior part of the foot of Nucella lapillus.

The method of opening barnacles thus appears to be very different from the drilling of large mussels and may well require some "learning", as described by Fischer-Piette. In the present study, the only very large barnacles found below MTL where dense Nucella populations were present were in rock spaces kept clear by Patella vulgata on a reef otherwise covered with mussels. Here it might be expected that the whelks had formed the habit of eating mussels and so ignored the few barnacles.

It was decided to test the possibility that the choice of larger, eroded barnacles in preference to the smoother newly settled individuals was due to a habit, developed after feeding in late autumn and early spring

on these older barnacles. The method of feeding was not different, as in the mussel-barnacle situation described above, but direct evidence was judged desirable. Therefore during observations in May, 1955, individuals feeding on older barnacles were marked with brown paint, and those feeding on newly settled barnacles with red. Of the 25 whelks marked as feeding on older barnacles, 1, 5, and 2 individuals were observed during the next three observations feeding on new barnacles. Conversely, of the 21 whelks originally feeding on new barnacles, 5, 7 and 3 were found feeding on older barnacles in the next three observations, respectively. Thus at least a quarter of the whelks changed the size of their prey over a period of three days. Thus the preference shown for older barnacles does not appear to be due to a preformed habit.

Discussion

A. Variations in the survival of Balanus balanoides.

Pearl and Miner (1935) state that "different species may differ in the age distribution of their dying just as characteristically as they differ in their morphology". It is clear also, from the results of the present study, that within one species, variation in survival is as characteristic as variation in morphology. Not only does the rate of mortality vary with age, season and locality, but also the causes of death change. The young barnacles are most affected by adverse physical factors which eliminate the individuals attached to exposed or unfavorable places. As the barnacles get older, these factors become less important and the mortality rate begins to become affected by biotic factors. Some of these are functions of population density, such as crowding, while others, such as predation, are determined by size and location. Occasionally, physical agents may affect older individuals, as was observed at high levels in April, 1955. Abrasion during storms may also be a cause of death at all ages.

The effect of storms was observed mainly on populations which had been heavily crowded previously, such

as those on Boulder 1 in 1953. In the absence of crowding and predation the survival was good, except at the upper levels during a hot period in April, 1955. This suggests that physical causes of mortality only act directly on older barnacles at high levels. The effect of the biotic factors increased toward the lower shore. The intertidal barnacle population could thus be visualized as being bounded by adverse physical factors at the top and adverse biotic factors at the bottom, all subject to variation with age and season.

These variations in mortality could be measured in Balanus balanoides because it was possible to obtain many accurate survival curves of different natural populations. In most studies of natural populations of animals, only an average estimate of mortality can be obtained. Deevey (1947) gave examples of many such studies; only Hatton (1938) had accurate survival data for several populations of the same species.

In the present study survival curves have been used in preference to the average expectation of life in presenting the data. Since the expectation of life represents an average figure for the whole life span measured, it will include all the changes in death rate which occur at different ages and seasons. For the

purpose of describing different causes of death it thus has little value. Deevey (1947) attempted to use it for this purpose to analyze the effect of crowding on survival in Balanus balanoides using the data of Hatton (1938). His Figure 8 suggests that the expectation of life of young barnacles was greatly affected by slight differences in crowding where this was very slight, but with greater degrees of crowding, the expectation remained constant. In this study it has been shown that at the same level survival decreases almost linearly with increasing density. In Deevey's figure, all the shore levels were included together. If the points for the highest level (near HWN) are omitted, no effect of crowding on longevity for any age is apparent. The large variation in longevity with changes in crowding is limited to the high levels only. From the results of the present study it is obvious that at all shore levels, crowding has a great effect on mortality. The effects of crowding in Deevey's analysis are masked by differences in later mortality, probably caused by other factors such as predation. The use of the calculated expectation of life as an index of survival led to erroneous conclusions, because it included various causes of death within one number. In the present

study it was used only in a limited way, as the average length of life within a relatively short span of time during which only one main cause of death was important.

In section V, it was shown that the populations at the upper and lower limits of the intertidal distribution of Balanus balanoides showed much greater differences between the strength of successive year classes than did those at mid shore levels. Annual variations in settlement were not great (Table 5.1) either at Millport or at St. Malo according to Hatton (1938), probably because the settlement density seems to be governed more by events on the settling surface than by the numbers of larvae in the plankton. The data from the present study supporting this conclusion have been given in section II; previous work by Pyefinch (1948) also tends to uphold this view. Therefore the only way in which the great differences between year groups could be brought about is by greater mortality after settlement at high and low levels. Other studies of year class fluctuations in marine species have tended to emphasize the planktonic larval period as the critical one, rather than the period after the animal begins its final stage as a bottom dweller or fish. The strength of year classes of certain fish seems to correlate very well with

the winds which tend to drift the larvae to or from proper areas. Therefore in these species the planktonic stage may be more critical, although little information is available on juvenile mortality.

B. The causes of mortality in natural populations.

Two principal difficulties are met with in considering causes of mortality. The first concerns the difficulty in measuring it accurately in nature. Deevey (1947) has analyzed this problem in detail; he pointed out that the only method which can be employed without accurate knowledge of the age structure of the population was that of identifying a group of individuals of known age and following their survival. Another problem is that the survival curves for different species usually begin at different stages in the life cycle, the larval period usually being missing.

The second difficulty, pointed out by Pearl and Miner (1935), concerns the problem of separating the intrinsic causes of mortality, such as genetic constitution and rate of activity, from the extrinsic ones originating in the environment.

Some of these difficulties were present in this study of a barnacle population; the planktonic stage was ignored, the survival curves beginning at settlement.

Also, nothing was known of the genetic constitution or rate of activity of the barnacles, and probably many environmental causes of death were ignored. On the other hand, the sessile nature of barnacles eliminated the errors in measuring survival, since the same group of individuals could be followed over a long period of time. Also, although the pelagic period was not included, the evidence indicates that the population density on the shore is fairly independent of mortality in the pelagic stage.

In evaluating the relative importance of the three variables which Pearl & Miner (1935) consider to be important in determining life duration, some information is available. The first variable, genetic constitution, undoubtedly accounts for some of the mortality in each group. There is probably no difference in the genetic constitution of the barnacle populations settling at different shore levels, however, since great mixing of larvae occurs in the plankton. Since the period of settlement is relatively short it is unlikely that the release of nauplii by barnacles of different genetic constitution at different times would lead to genetic separation of the settled larvae. Differential mortality

due to differences in the environment might produce genetically different populations at different levels after settlement. But the great differences observed in the survival of populations from nearby areas can probably not be ascribed to variation in original genetic constitution.

Pearl and Miner give evidence that the rate of living (including growth, reproduction, motor activity, etc.) is inversely correlated with longevity. The rate of cirral beat of barnacles has been measured by Southward (1955) in England and Wales. Chthamalus stellatus showed a higher rate at lower shore levels from only one of the four locations studied. Balanus balanoides had a faster rate at lower levels one day after collection, but after two or three days in the laboratory, no differences in rate were found between barnacles from different levels. Which of these findings illustrates the activity under natural conditions is not known. Some observations of Balanus balanoides were made on the shore at Millport just after the rising water level had covered them. These observations suggest that when there is any water motion, as there usually is in the intertidal zone, the feeding activity is not characterized by any regular cirral beat, but rather that the cirri

are held open for varying lengths of time, up to 12 seconds, before retraction. This seems to indicate that retraction results when a particle is caught; the cirral activity would thus be a function of the amount of food available. At the present time it is impossible to decide how barnacles at different levels or locations differ in their rate of activity. Segal, Rao and Thompson (1953) found that limpets from lower shore levels had persistently higher rates of heart beat after three days in the laboratory. Mussels from lower levels were found to have faster rates of water propulsion; these differences persisted for weeks in the laboratory, although acclimation was achieved within a month when limpets were transplanted in the field. Although it seems likely that the rate of activity of barnacles is greater at low shore levels, the only positive evidence is that growth is faster there. Whether this has any effect on longevity cannot be decided with the present data.

The third variable, environment, appears to be the most important in determining the variations in survival observed in this study. This is illustrated in Figure 10, for the 1954 settlement on Boulder 6, low on the shore. The survival there was very good, except

for the period of intense predation in the autumn, shown in Figure 14; the density was low and crowding was not serious. At high shore levels, as shown in Figure 13, the only serious mortality after one year of age was correlated with an unusual environmental condition. When deleterious environmental factors were not operating, the mortality, presumably from intrinsic biological causes, was very small.

In considering the comparative mortality of different species, Pearl and Miner (1935) have classified survival curves into three general types, according to whether the rate of mortality is heavier at the beginning or end of life, or is relatively constant throughout. The present study provides an opportunity to describe the variation in the types of survival curves within one species. This determination of intra-species variation is important, since it helps to decide whether inter-species variations are significant. Deevey (1947), expressed the difference between the types as the ratio of the maximum to the average life span. This ratio has been used in the present analysis, as given in Table 7.1. Hatton's (1938) data are included, and for this comparison, only the highest and lowest shore levels from both studies were used. For purposes of classification,

Table 7.1 - The ratio of the maximum life span to the average for populations of *Balanus balanoides* at the upper and lower limits of distribution on the shore.

Location and Authority	Level	Area	Calculated from settlement onward			Calculated from spawning, assuming a mortality of 90% up to settlement.		
			Average expectation in months	Maximum span in months	Maximum / Aver.	Aver. expectation	Maximum span	Maximum / Aver.
Millport	HWN	Area 2	3.8	60	15.5	0.9	61	68.0
Present study, 1953 settlement	Between MTL and LWN	Boulders 1	4.1	8.2	2.0	0.9	9.2	10.1
		2	2.8	10.4	3.7	0.8	11.4	14.1
St. Malo, France Hatton (1938)	HWN Level II	Decolle Ouest	11.0	60	5.4			
		Decolle Est	23.1	60	2.6			
		Cite	14.3	60	4.2			
1930 settlement	LWN Level IV	Decolle Ouest	12.6	27.0	2.2			
		Decolle Est	9.5	21.0	2.2			
		Cite	11.2	27.5	2.4			

Note: The average expectation of life for the populations studied by Hatton (1938) was taken from Deevey (1947); it was calculated for the high level populations (Level II) on the assumption that the maximum span was five years. The same assumption was made for the Area 2 data at Millport.

Deevey tentatively ascribed the ratios 2.0 to 6.0 to his type I, where most of the death occurs late; ratios from 6 to 15, indicating more or less equal mortality rates throughout life, were classed as Type II. When there is heavy early mortality, the few survivors of which live a relatively long time, the curve is classed as Type III, with ratios greater than 15.

Hatton's curves were all of Type I, although the ratio was greater at high levels. In the present study, the ratios, calculated from settlement onward, as with Hatton's data, indicated Type I at the low level and Type II at high level. If the planktonic phase is included, assuming a ninety percent mortality in the month's pelagic life, the lower levels become Type II, the upper levels extreme Type III. Since the assumed pelagic mortality is probably an underestimate, and the assumption conservative that the maximum life span is only five years at high levels, the ratios are probably minimum estimates. Nevertheless they indicate the variability which may exist in different parts of the species' range. This suggests that before a comparison between different species on the basis of this classification can be made, some idea of the variability within each species should be obtained.

Summary

The accessibility and the sessile nature of intertidal barnacle populations allowed very accurate records to be made of recruitment and survival. With experimental modification of some of the environmental conditions, the causes of some of the observed population changes could be determined.

During the period studied, the supply of larvae was always more than adequate to populate the area. The settlement density of each year class appeared to be determined by conditions on the shore rather than by the supply of larvae from the plankton. The larvae settled first near the surviving adults; later settlers, forced to attach in less favorable places, suffered greater mortality.

This early mortality of newly settled barnacles was closely correlated with warm weather and storms. The damage from storms destroyed more of the later settlers than of the earlier ones. Limpets also killed young barnacles, but whelk predators ignored the young settlement if there were adults present.

Crowding occurred in moderately dense populations as growth began. In the first growing season, mortality increased with increased density. Since the relative growth rate was faster at low shore levels, crowding was more intense here than at higher levels at the same density. At the low levels, distortion of form resulted from intense crowding; these barnacles were usually lost in later storms, since they were poorly attached. This introduced a lag in the effects of crowding on mortality.

Much of the mortality in crowded populations was caused by direct action between neighboring individuals. This was manifested in undercutting and displacement, smothering, or lateral crushing. After the age of eighteen months, when growth had practically ceased, crowding was negligible, although a few instances of younger barnacles smothering older ones were observed.

A cyclic sequence of events, regulated by the density of the barnacle population, was observed at low shore levels. Here heavy or light settlements were correlated with the presence or absence of adults, respectively. This was a result of the cyprids being stimulated to attach by the presence of adults. However, the adults were eliminated after heavy settlements, when they developed the unstable growth form described previously. The following settlement was then light, since there were few adults present to stimulate attachment. Thus an internally regulated cycle is suggested.

Dominant year classes occurred at the upper and lower intertidal distribution limits of Balanus balanoides. These were shown to result from differences in the mortality after settlement and not from variations in the pelagic larval supply, as has been postulated for other marine species.

The age structure of the barnacle population varied at different shore levels. At high levels, four or more year classes may exist together, whereas at lower levels, only two year classes were found, and at times, only one. This situation has been shown to be the result of the action of biological

factors partly dependent on the density of the barnacles. Experiments using two different methods have shown that the whelk predators, Nucella lapillus L., select the larger barnacles as prey. By excluding the whelks from small areas of barnacles at mid shore levels, the age structure observed at high levels was produced lower down. From the results of two different methods of measuring the feeding rates of Nucella, it appears that this species is the only important predator of Balanus balanoides at this location.

The effect of predation selective for larger sized barnacles was suggested to be the reason for the conflicting results found in the various growth studies of Balanus balanoides. The assumption usually made by students of growth, that mortality is random with regard to size under natural conditions, may not be true.

Variation between the survival curves under various conditions of this one species has been shown to be as great as that found by earlier studies between the curves of different species.

APPENDIX

These consist of the total numbers counted on the given area of rock surface ($cm.^2$), for each year class on each census square. These are the numbers, which, when reduced to the number on a standard area, (either twenty-five or one $cm.^2$), appear as the initial number of each survival curve given in the Figure indicated. With one exception, the counts refer only to barnacles attached directly to the rock; the post-settlement counts in 1953 on Area 1 were not so distinguished at the time.

Square No.	Ht. from MTL in feet	Ave. % time in air	Figure No. and: Symbol	Successive year classes									
				Pre-1952		1952		1953 (end of set)		1953 (Autumn)		1954 (end of set)		1955 (end of set)	
				Area	No.	Area	No.	Area	No.	Area	No.	Area	No.	Area	No.
						Area 1, Upper level.									
Cage 1.	2.6	75	16: 1	29.0	101	5.0	92	1.7	171	1.6	10	2.5	178	3.9	255
Cover	"	"	16: A	28.7	102	3.5	21	1.4	161	21.6	94	7.5	277	3.9	232
Control 1.	"	"	16: B	28.5	98	4.0	19	2.2	242	14.5	120	15.8	580	3.5	174
Control 2.	"	"	16: D	49.3	29	39.7	21	-	-	37.3	131	11.5	284	-	-
Cage 2.	"	"	16: 2	-	-	65.9	22	-	-	56,9	123	17.3	470	1.0	42
Cage 3.	"	"	16:C-3	51.3	90	26.5	14	-	-	24.9	119	17.5	232	2.5	125
						Area 1., Middle level.									
Cage 1.	2.1	69	17: 1	29.5	63	8.7	47	1.8	213	9.3	22	3.4	223	2.1	151
Cover	"	"	17: A	29.0	51	9.9	77	1.9	116	28.7	100	25.8	636	4.0	168
Control 1.	"	"	17: B	29.0	47	7.9	44	1.9	177	26.5	106	25.1	529	5.1	201

Square No.	Ht.	%	Figure	Pre-1952 Area	Pre-1952 No.	1952 Area	1952 No.	1953 Area	1953 No.	1953 Area	1953 No.	1954 Area	1954 No.	1955 Area	1955 No.
						Area 1., Middle level									
Control 2.	2.1	69	17: C	46.6	35	36.4	28	-	-	33.2	190	16.7	348	-	-
Cage 2.	"	"	17: 2	92.2	43	80.5	32	-	-	76.9	279	17.4	395	3.8	205
Cage 3.	"	"	17: 3	98.5	8	96.3	64	-	-	89.0	635	8.1	164	-	-
Cage 4.	"	"	17:D-4	98.5	4	97.4	33	-	-	93.6	516	30.5	426	-	-
						Area 1., Lower level									
Cage 1.	1.5	63	18:	-	-	61.2	100	-	-	49.8	421	13.4	320	2.0	129
Control 3.	"	"	18: A	-	-	25.3	142	3.0	95	22.7	66	25.3	245	2.2	98
Control 1.	"	"	18: B	-	-	29.0	202	2.9	119	22.0	159	24.7	292	7.8	339
Control 2.	"	"	18: C	-	-	52.1	44	-	-	46.1	327	18.1	367	4.0	166
						Boulders, below MTL									
Boulder 1.	-0.9	42	10	-	-	25.0	24	25.0	464	-	-	47.3	678	9.0	252
Boulder 2.	- 0.9	43	10	-	-	25.	6	25.	390	-	-	52.6	496	9.0	232
Boulder 5a.	- 1.8	35	10	-	-	-	-	49.	443	-	-	47.1	889	9.0	247
Boulder 5b.	- 1.9	34	10	-	-	-	-	-	-	-	-	87.5	87	-	-
Boulder 6a.	- 1.8	35	10	-	-	-	-	-	-	-	-	51.4	539	9.0	216
Boulder 6b.	- 1.9	34	10	-	-	-	-	49.	506	-	-	59.4	373	9.0	198

Square No.	Ht.	%	Figure	Pre-1952 Area	Pre-1952 No.	1952 Area	1952 No.	1953 Area	1953 No.	1953 Area	1953 No.	1954 Area	1954 No.	1955 Area	1955 No.
							Area 2., near HWN								
All three squares:	4.2	91	13	75.0	6	75.0	283	20.0	676	75.0	20	6.0	82	3.0	55
							Experimental Stones								
Stone 1.	- 0.9	42	10					9.0	605			13.5	694	4.0	264
Stone 2.	"	"	10					11.2	410			4.7	583	4.0	188
Stone 3.	1.1	59	9					5.6	335			6.5	505	4.0	280
Stone 4.	"	"	9					4.7	442			5.0	523	4.0	304
Stone 5.	2.5	74	-					9.0	178			4.5	62	-	-
Stone 6.	"	"	-					7.0	84			4.0	60	-	-
Stone 7.	2.2	70	9					4.5	337			6.6	665	6.5	932
Stone 8.	"	"	9					4.7	217			6.5	624	3.6	462

Note: The numbers given for the stones are the total numbers which attached during the settlement season. The number at the end of the season can be calculated using the percentage mortalities during the season as listed in Table 3.3.

LITERATURE CITED

Allee, W.C., A.E. Emerson, O. Park, T. Park and K.P. Schmidt, 1949. The Principles of Animal Ecology. W.B. Saunders Co.

Barnes, H., 1953a. Size variations in the cyprids of some common barnacles. J. Mar. Biol. Ass. U. K. 32, 297-304.

Barnes, H., 1953b. Orientation and aggregation in Balanus balanus (L.) Da Costa. J. Anim. Ecol. 22, 141-148.

Barnes, H., and H.T. Powell, 1950. The development, general morphology and subsequent elimination of barnacle populations, Balanus crenatus and B. balanoides, after a heavy initial settlement. J. Anim. Ecol. 19, 175-179.

Barnes, H. and H. T. Powell, 1953. The growth of Balanus balanoides (L.) and B. crenatus Brug. under varying conditions of submersion. J. Mar. Biol. Ass. U. K. 32, 107-128.

Bousfield, E.L., 1954. The distributions and spawning seasons of barnacles on the Atlantic Coast of Canada. Bull. Nat. Mus. Can. 132, 112-154.

Carruthers, J. N., 1938. Fluctuations in the herrings of the East Anglian autumn fishery, the yield of the Ostend spent herring fishery, and the haddock of the North Sea--in the light of relevant wind conditions. Rapp. Cons. Explor. Mer. 107, 10-15.

Carruthers, J. N., A. L. Lawford, V.F.C. Veley and B.B. Parrish, 1951. Variations in brood-strength in the North Sea haddock in the light of relevant wind conditions. Nature, Lond. 168, 317-19.

Chase, Joseph, 1953. A study of the winds and temperatures in relation to the brood strength of Georges Bank haddock. Unpub. Manuscript, ref. no. 53-67, Woods Hole Oceanog. Inst.

Chipperfield, P. N. J., 1948. Unpublished PhD. thesis, Liverpool University, England.

Corlett, J., 1948. Rates of settlement and growth of the "pile" fauna of the Mersey estuary. Proc. Lpool. Biol. Soc. 56, 2-28.

Crisp, D.J. and E. W. Knight-Jones, 1953. The mechanism of aggregation in barnacle populations. J. Anim. Ecol. 22, 360-362.

Crisp, D.J. and H. Barnes, 1954. The orientation and distribution of barnacles at settlement with particular reference to surface contour. J. Anim. Ecol. 23, 142-162.

Crisp, D. J. and P. A. Davies, 1955. Observations *in vivo* on the breeding of *Elminius modestus* grown on glass slides. J. Mar. Biol. Ass. U. K. 34, 357-80.

Darwin, Charles, 1854. A monograph of the sub-class Cirripedia. London, Ray Society.

Deevey, E. S., Jr., 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22, 283-314.

Elmhirst, R., 1923. Notes on the breeding and growth of marine animals in the Clyde Sea Area. Rep. Scot. Mar. Biol. Ass. 1922.

Fischer-Piette, E., 1935. Histoire d'une mouliere. Bull. Biol. 69, 152-177.

Fretter, V., 1946. The pedal sucker and anal gland of some British Stenoglossa. Proc. Malac. Soc. Lond. 27, 126-130.

Hartley, P. H. T., 1949. Blennies and the ecology of littoral fishes. Challenger Soc. Lond. 3: 1949, 19. (an abstract)

Hatton, Harry, 1938. Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. Ann. Inst. oceanogr. Monaco, 17, 241-348.

Hatton, Harry and E. Fischer-Piette, 1932. Observations et experiences sur le peuplement des cotes rocheuses par les Cirripedes. Bull. Inst. oceanogr. Monaco 592, 1-15.

Hjort, Johann, 1914. Fluctuations in the great fisheries of Northern Europe. Rapp. Cons. Explor. Mer 20, 1-228.

Hjort, Johann, 1926. Fluctuations in the year classes of important food fishes. J. Cons. int. Explor. Mer 1, 1-38.

Knight-Jones, E. W., 1953a. Laboratory experiments on gregariousness during setting in Balanus balanoides and other barnacles. J. Exp. Biol. 30, 584-598.

Knight-Jones, E. W., 1953b. Decreased discrimination during setting after prolonged planktonic life in larvae of Spirorbis borealis (Serpulidae). J. Mar. Biol. Ass. U. K. 32, 337-345.

Knight-Jones, E. W. and D. J. Crisp, 1953. Gregariousness in barnacles in relation to the fouling of ships and to anti-fouling research. Nature, Lond. 171, 1109.

Kuznetzov, W. W. and T. A. Matveeva, 1949. The influence of the density of the populations on certain biological processes in Balanus balanoides. (L.) from Eastern Murman. C. R. Acad. Sci. U. R. S. S. 64, 3.

Lack, David, 1951. Population ecology in birds. A review. Proc. X Int. Orn. Cong. 1950, 409-48.

Miller, M. A., J. C. Rapean and W. F. Whedon, 1948. The role of slime film in the attachment of fouling organisms. Biol. Bull. Woods Hole 94, 143-157.

Moore, H. B., 1934. The biology of Balanus balanoides. I. Growth rate and its relation to size, season and tidal level. J. Mar. Biol. Ass. U. K. 19, 851-68.

Moore, H. B., 1935. The biology of Balanus balanoides. IV. Relation to environmental factors. J. Mar. Biol. Ass. U. K. 20, 263-308.

Moore, H. B., 1936a. The biology of Balanus balanoides. V. Distribution in the Plymouth Area. J. Mar. Biol. Ass. U. K. 20, 701-16

Moore, H. B., 1936b. The biology of Pupura lapillus. I. Shell variation in relation to environment. J. Mar. Biol. Ass. U. K. 21, 61-89.

Moore, H. B., 1938a. The biology of Pupura lapillus. Part II. Growth. J. Mar. Biol. Ass. U. K. 23, 57-66.

Moore, H. B., 1938b. The biology of Pupura lapillus. Part III. Life history and relation to environmental factors. J. Mar. Biol. Ass. U. K. 23, 67-74.

Nicholson, A. J., 1954. Environmental demonstrations of balance in populations. Nature, Lond. 173, 862.

Parke, M. W. and H. B. Moore, 1935. The biology of Balanus balanoides. II Algal infection of the shell. J. Mar. Biol. Ass. U. K. 20, 49-56.

Parrish, B. B., 1950. Brood fluctuations in the North Sea haddock population. Challenger Soc., Lond. 3, 18. (an abstract).

Pyefinch, K. A., 1948. Notes on the biology of Cirripedes. J. Mar. Biol. Ass. U. K. 27, 464-503.

Pyefinch. K. A. and J. C. Mott, 1948. The sensitivity of barnacles and their larvae to copper and mercury. J. Exp. Biol. 25, 276-298.

Quayle, D., 1952. The rate of growth of Venerupis pullastra (Montagu) at Millport, Scotland. Proc. Roy. Soc. Edinb. B. 64, 384-406.

Rice, Lucille A., 1935. Factors controlling arrangement of barnacle species in tidal communities. (in: Some marine biotic communities of the Pacific Coast of North America.) Ecol. Monogr. 5, 293-304.

Runnstrom, S., 1925. Zur biologie und entwicklung von Balanus balanoides (Linne). Univ. Bergen Arb. naturv. R. 5, 1-46.

Schafer, W., 1938. Die geologische Bedeutung von Bohr-Organismen in tierischen Hart-Teilen, aufgezeigt an Balaniden - Schill der Innenjade. Senckenbergiana 20, 304-313.

Schafer, W., 1948. Wuchsformen von Seepocken (Balanus balanoides). Natur u. Volk 78, 74-78.

Segal, E., K. P. Rao, and T. W. James, 1953. Rate of activity as a function of intertidal height within populations of some littoral molluscs. Nature, Lond. 172, 1108-9.

Sette, O. E., 1943. Biology of the Atlantic mackerel (Scomber scombrus) of North America. Part 1: Early life history, including growth, drift, and mortality of the egg and larval populations. Fish. Bull., U. S. 50 (38), 147-237.

Sokolova, M. N., 1951. Influence of the conditions of the environment on the density of the colony and the shape of the shell in Balanus balanoides. C. R. Acad. Sci. U. R. S. S.,N. S. 78, 1227-1230. (In Russian, 4 illus.)

Southward, A. J., 1953. The ecology of some rocky shores in the south of the Isle of Man. Proc. Lpool. Biol. Soc. 59, 1-50.

Southward, A. J., 1955. On the behaviour of barnacles. II. The influence of habitat and tide-level on cirral activity. J. Mar. Biol. Ass. U. K. 34, 423-33.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25, 1-45.

Trusheim, F., 1932. Palaontologisch Bemerkens-wertes aus der Okologie rezenter Nordsee-Balaniden. Senckenbergiana 14, 70-87.

Walford, L. A., 1938. Effects of currents on distribution and survival of the eggs and larvae of the haddock (Melanogrammus aeglefinus) on Georges Bank. Bull. U. S. Bur. Fish. 29.

Weiss, C. M., 1948. Seasonal and annual variations in the attachment and survival of barnacle cyprids. Biol. Bull. Woods Hole 94, 236-243.

Woods Hole Oceanographic Institution, 1952. Marine fouling and its prevention. U. S. Naval Institute, Annapolis, Maryland. (W.H.O.I. contribution No. 580)

Zenkewitch, L. A., 1935. Some observations on fouling in Ekaterininskaya Bay (Kola Fjord, Barents Sea). Bull. Soc. Nat. Moscou 44, 103-112.

Bassindale, R., 1936. The developmental stages of three English barnacles, Balanus balanoides (Linn.), Chthamalus stellatus (Poli) and Verruca stroemia (O.F.Muller). Proc.Zool. Soc. Lond., 1936, 57-74.